FROM ECOPHYSIOLOGY TO ECOREGIONS: INTEGRATING PATTERNS IN WATERFOWL REPRODUCTIVE SUCCESS ACROSS MULTIPLE SCALES

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By

David William Johns

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Dean
College of Graduate and Postdoctoral Studies
University of Saskatchewan
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Saskatoon, Saskatchewan Canada
S7N 5C9

ABSTRACT

Variation in avian reproductive success (RS) can be influenced by intrinsic traits (e.g., individual quality, physiology and experience) or extrinsic factors (e.g., weather, habitat use, or landscape composition) which can act across multiple scales. Determining how these two factors affect RS – and how they interact – represent significant challenges for ecologists and conservationists. Thus, I evaluated these two main hypotheses using information obtained for northern pintail (*Anas acuta*) and mallard (*Anas platyrhynchos*) breeding in the Canadian prairies. I integrated data from laboratory experiments, field-based observational studies and existing long-term datasets to determine the relative importance of intrinsic (past and current metrics of individual quality) and extrinsic (landscape composition) factors in contributing to variation in RS for prairie-breeding ducks at multiple scales. I also validated and used feather biomarkers to investigate evidence of energetic carry-over effects on reproductive performance in both species.

To verify that an individual's feather corticosterone ($CORT_f$) levels are related to energy expenditure, I manipulated work rates of mallard ducklings in the laboratory. Ducklings experiencing higher workloads had lower body mass, slower growth rates, greater daily energy expenditure and higher $CORT_f$. These patterns were repeatable and $CORT_f$ reflected current energetic demands during feather replacement.

Using $CORT_f$ and stable isotopes in feathers, I provided new insights regarding the consequences of migratory origins of adult female pintails breeding in southern Saskatchewan, and found no evidence of strong carry-over effects on pre-breeding body condition or reproductive investment. However, late-nesting females were typically from coastal wintering regions and had higher $CORT_f$ in body feathers grown during winter-spring, suggesting that energetic challenges during body moult during late winter or early spring migration delayed timing of breeding.

I investigated maternal influences on RS and found that pintail duckling survival was higher among breeding females with lower late-incubation body mass, those that hatched nests somewhat later in the season or behaved more cautiously during brood rearing. Extrinsic landscape conditions drove most variation in duckling survival. Duckling survival was higher in grassland-dominated landscapes and, in agricultural landscapes, broods hatching from winter

wheat had similar survival to perennial cover, double the estimates in spring-seeded cropland. Ducklings raised in local environments with higher amounts of perennial cover and seasonal wetlands, but lower amounts of wetland edge, had higher survival. On balance, the benefits of higher nest survival in winter wheat were not completely superseded by lower duckling survival for broods raised in intensive agricultural areas.

Using unique data sets composed of individually-marked adult female mallards, I did not find any consistent indication that $CORT_f$ was correlated with either reproductive effort or success, or local weather and wetland conditions, in the same year as feather growth. Counter to initial predictions, I found that current RS was unrelated to $CORT_f$ levels in feathers grown the previous summer-fall. Path analyses of mallard breeding decisions revealed that lighter females were less likely to breed but experienced higher hatching and fledging success; female age had no direct effects on the decision to breed nor directly influenced fledging success. As expected, greater nesting effort and investment occurred on sites with a higher pond abundance and above-average regional pond conditions.

For breeding mallards, heavier females were more likely to settle in areas with above-average pond conditions, nested earlier and re-nested more often while females that had lower $CORT_f$ in wing feathers tended to re-nest more often but experienced higher nest success. Older birds, and those that settled in areas with more grassland, had larger clutch sizes. As expected, nest success was higher on sites with a higher abundance of ponds and above-average regional pond conditions but lower for early and re-nests, with the number of hatched young smaller for late or re-nests. Overall, fledging success was higher in late-hatched or larger broods and of successful nests, more ducklings fledged if it was a re-nest but there were trade-offs with pond abundance and egg production.

Overall, in pintails and mallards, local environmental factors and landscape composition had consistently strong effects on RS whereas measurements of individual quality were generally weaker or more variable. Through integration of intrinsic and extrinsic factors, I bridged our understanding of variation in energetic conditions and RS across ecological, spatial and temporal scales. Further study is required to evaluate the roles of carry-over effects on prairie-breeding ducks, as this would more clearly reveal putative linkages between conditions on non-breeding areas and subsequent RS.

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Finally, thank you to my wife Cathy. Words alone will never be enough to express my gratitude for all you have given and provided me over these years. The sacrifices you have made to support me during this path extent beyond the lonely kilometers travelled and sunrise to sunset workdays just to spend time with me, or all of the lonesome and challenging moments to enable me to “finish school”. No one is more patient, perfect or unwavering; I share this with you and look forward to the decades ahead.

DEDICATION

I dedicate this dissertation to my children. Your endless enthusiasm and curiosity inspire me every day. Remember that no matter how hard or difficult the path ahead may seem, you are capable of anything. Be curious, ask questions, believe in yourself and never give up on your goals.

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CHAPTER 1. INTRODUCTION

1.1 General Introduction

A central focus in landscape ecology is the study of interactions between organisms and their environment such as how the quality, arrangement and composition of both habitats and landscapes influence reproductive effort, survival and ultimately fitness. Interactions between the environment and components of fitness such as reproductive success are often dynamic and context dependent, where the strengths or directions of relationships change between habitat types, individuals or through time. Reproductive success is the primary driver of waterfowl population dynamics in the Prairie Pothole Region (PPR) of North America and is a product of nesting success and the survival of females and ducklings (Johnson et al. 1992, Hoekman et al. 2002, Koons et al. 2006, Mattsson et al. 2012). Understanding sources of variation in waterfowl reproductive success not only informs management actions to conserve waterfowl populations but contributes to an improved understanding of avian reproductive ecology. Previous studies have focused on how landscapes influence waterfowl habitat selection and nesting success, due to the direct relevance of these variables to wildlife management applications (Clark and Nudds 1991, Horn et al. 2005, Stephens et al. 2005). More recently, research has shifted to understand factors driving variation in offspring survival and associations with landscape attributes (Amundson and Arnold 2011, Bloom et al. 2012).

A number of sources contribute to variation in reproductive success across both local and broad spatial scales, including: individual quality as measured through physiology or condition, past history, behaviour and experience, as well as environmental factors such as food availability, weather, or the composition and configuration of the surrounding landscape (Afton and Paulus 1992, Harrison et al. 2011, Chalfoun and Schmidt 2012). Understanding how and why reproductive success varies across spatial, ecological and temporal scales will enhance our knowledge of avian reproductive ecology and enable refinement of management strategies. For example, factors which influence fitness at regional or landscape scales may not have the same driver, magnitude or direction when considered at local scales (Wiens 1989, Turner et al. 2001, Fairhurst et al. 2013b). Just as levels of spatial scale range from centimeters-to-kilometers or habitat patches to eco-regions, we can also consider both intrinsic and extrinsic processes acting along ecological scales ranging from an individual's physiological response to constraints of

habitats or landscapes, and even broad scale regional effects such as climate or wintering periods, which combine both space and time (Figure 1.1). Using a landscape ecology perspective and linking both intrinsic and extrinsic factors contributing to variation in reproductive success across ecological, spatial and temporal scales, this dissertation uses an integrated approach to examine sources of variation in reproductive success and investigate their ramifications for waterfowl management.

1.1.2 Intrinsic Contributions

Intrinsic factors such as individual age, body condition, and timing of reproduction can influence reproductive investment in waterfowl (Dzus and Clark 1998, Guyn and Clark 1999, Blums et al. 2002, Devries et al. 2003, Arnold et al. 2012). Older females may be able to utilize past experience to secure higher quality habitat, resources, or devote more time to brood rearing, conferring survival or growth benefits to offspring. Birds with greater internal resources may be able to out-compete conspecifics, breed earlier and devote more time to brood rearing (Blums et al. 2005), or invest more in reproduction and buffer energetic demands of higher investment (Bonier et al. 2009a). Older females are typically larger than younger individuals and may be capable of securing better quality habitats, earlier hatch dates and higher reproductive success (Afton and Paulus 1992, Yerkes 2000, Blums et al. 2002, Devries et al. 2003), yet results are not always consistent for duckling survival (Guyn and Clark 1999, Amundson et al. 2011).

While individual state has typically been assessed using measures of body mass (Bêty et al. 2003, Labocha et al. 2012), alternative indices such as physiological measurements of hormones like corticosterone (Bonier et al. 2009, Anelier et al 2010) may provide further insight into differential states beyond mass alone. Corticosterone (CORT) is a glucocorticoid hormone secreted by the hypothalamic-pituitary-adrenal axis whose primary purpose is energy regulation (Landys et al. 2006). Baseline levels of CORT are often positively associated with environmental challenges and negatively relate to fitness; however, energetic demands that increase fitness, such as reproduction, can also have a positive relationship with CORT (Bonier et al. 2009a). Variation in CORT has been related to habitat quality, weather, personality, reproductive performance and survival (Marra and Holberton 1998, Marra et al. 1998, Angelier et al. 2007, Cockrem 2007, Bonier et al. 2009b). Studies of CORT have identified the importance of intrinsic quality on hormonal response of corticosterone (Bonier et al. 2009b, Angelier et al. 2010).

In birds, CORT is incorporated into feather tissue ($CORT_f$) during its growth, representing a record of both baseline and acute energetic responses over a period of days to weeks (Bortolotti et al. 2008) and persists with the bird until the feather is moulted. The ability for feathers to incorporate levels of circulating CORT over different seasons provides a unique method to apply this biomarker to index individual quality, examine its influences across spatial or temporal scales, and investigate COEs. The collection of feathers grown during critical life cycle stages provides opportunities to look at antecedent factors influencing reproductive success and assess if long-lasting impacts on future reproduction exist.

Individuals display consistent differences in behavioural responses across time and contexts, through both single behaviours and suites of correlated responses such as boldness, aggression or exploratory behaviour (Sih et al. 2004, Dingemanse and Réale 2005, Dingemanse and Wolf 2010). The adaptive advantages of consistency are variable across environments, where aggression can assist in securing resources, competition for mates or defending offspring, yet maladaptive for avoiding predation, offspring care or in rapidly changing environments (Sih et al. 2004), and can ultimately influence reproductive success and fitness (Sih et al. 2004, Groothuis and Carere 2005, Boos 2007). The adaptive benefits of aggressive traits on offspring survival have been demonstrated across several species, including mammals (Boon et al. 2007), reptiles (Sinn et al. 2008), and avian species (Kontiainen et al. 2009, Betini and Norris 2012, Patrick and Weimerskirch 2014). However, the roles of maternal behaviour such as aggression, boldness and syndromes along the bold/shy or proactive/reactive continuum and its contributions towards offspring survival are yet to be tested.

1.1.3 Extrinsic Contributions

Habitat selection theory predicts that animals should choose habitats that improve survival and reproductive success (Fretwell and Lucas 1969). Extrinsic factors such as the surrounding habitat can impact reproductive success through multiple pathways, including direct and indirect effects of limited habitat availability or functional quality where insufficient breeding sites, foraging locations, or habitats with low predation risk may reduce reproductive success. Indirectly, individuals in poorer quality habitats may require greater effort to secure resources or avoid predation, resulting in reduced ability to allocate resources to breeding or parental care. The ability to study the direct interaction between survival and habitat selection at

multiple scales could greatly enhance our understanding of the complex consequences of habitat choice (Bloom et al. 2013).

Differences in landscape type, structure, configuration and composition may also affect survival. Brood survival in grassland-dominated landscapes appears to be higher than cropland-dominated landscapes (Guyn and Clark 1999, Peterson 1999). Increasing proportions of grassland and larger grassland patches are associated with increases in duck nesting success in a nonlinear fashion (Horn et al. 2005, Stephens et al. 2005), yet mallard ducklings show decreased survival when broods are near perennial cover (Amundson and Arnold 2011, Bloom et al. 2012), as larger amounts of perennial cover may support larger and diverse predator communities (Phillips et al. 2003).

For waterfowl broods, selection at the landscape level scale (2nd order selection; Johnson 1980) influences survival rates, with elevated survival in intact grasslands relative to agricultural landscapes (Guyn and Clark 1999, Peterson 1999, Richkus 2002). However, more localized effects of upland habitats such as perennial cover on brood survival do not always match broad landscape patterns (Amundson and Arnold 2011, Bloom et al. 2012) or are counter to results from nest survival (Klett et al. 1988, Howerter et al. 2008). This relationship highlights the context-specific nature of examining environmental effects where habitats that support one life cycle stage may not have the same effects for later stages. Habitat, which are attractive for early nesting, have been shown to have higher nest survival rates and may provide survival advantage to young (Guyn and Clark 1999, Krapu et al. 2000, Amundson and Arnold 2011).

Positive relationships between pond abundance and duckling survival (Dzus and Clark 1998, Pietz et al. 2003, Krapu et al. 2006, Amundson and Arnold 2011, Bloom et al. 2012) and use (Dzus and Clark 1997, Raven et al. 2007) are often consistent. Differences in the amount of wetland, types of wetlands and intra-wetland characteristics between cropland-dominated and grassland-dominated landscapes may cause variation in duckling survival. At the wetland level scale (3rd order selection; Johnson 1980), wetlands provide critical brood-rearing habitat, where the type and arrangement of wetlands is shown to have consequences for survival (Rotella and Ratti 1992a,b, Bloom et al. 2012). Because of agricultural intensification, many smaller temporary wetlands have been removed from the landscape and water in some cases has been drained into basins that are more permanent. The composition and configuration of wetlands may

affect survival through provision of food, and protection from inclement weather and/or predators (Sedinger 1992). Higher pond abundance or density may enable females to move their brood shorter distances overland in response to changing food resources, competition or predation pressures (Krapu et al. 2006), or provide greater availability of resources accessible to broods. Similarly, the amount, type and spatial arrangement of emergent vegetation within a pond may play an important role for the survival of ducklings. Peterson (1999) found that emergent vegetation was an important predictor of pintail duckling survival while Bloom et al. (2012) found that mallard duckling survival was higher when vegetation existed in a ring configuration.

Most studies examining landscape effects focus on composition rather than configuration. Habitat fragmentation may increase predator foraging in smaller patches and is hypothesized to reduce grassland bird populations (Herkert et al. 2003). However, drivers of population reduction through fragmentation remains unclear and while studies have addressed these concepts regarding nesting success (Chalfoun et al. 2002, Stephens et al. 2005), impacts of grassland fragmentation and wetland proximity on duckling survival have not been addressed.

1.1.4 Carry-over Effects

While investigations of how environmental conditions (i.e. habitat, climate) influence performance metrics such as survival or reproductive success are widespread, many are limited to intra-seasonal effects (i.e. how breeding habitat influences breeding success). Environmental factors outside of breeding periods may influence future reproduction or survival, such as reductions in habitat quality (Marra et al. 1998, Norris et al. 2004), food resources (Sorensen et al. 2009) or changes in climatic conditions (Constantini et al. 2010). Migratory species such as waterfowl utilize different habitats and landscapes throughout seasons, each with variable conditions. Interactions in one location or time period can also alter the performance of individuals in subsequent periods (Ankney and MacInnes 1978, Raveling 1979, Raveling and Heitmeyer 1989). Termed carry-over effects (COEs) these processes alter the state or condition of an individual as it transitions between periods (i.e. seasons) and impacts individual performance in subsequent periods (Norris 2005, Norris and Marra 2007, Harrison 2011, Sedinger and Alisauskas 2014).

In the face of environmental change, an individual's response should be discernible prior to population level response, meaning the measurement of physiological and intrinsic responses can provide insight into its contributions to reproductive success earlier than population level demographic change alone (Marra and Holberton 1998, Ellis et al. 2012). Energy availability plays a major role in facilitating shifts in individual states, which may delay the timing of breeding or reduce reproductive success and survival in subsequent seasons. Variation in habitat quality (Studds and Marra 2005, Norris and Taylor 2006, Norris and Marra 2007, Inger et al. 2010), food quality (Sorensen et al. 2008), size of endogenous reserves (Ebbinge and Spaans 1995), as well as unexpected storms, weather or past reproductive investment are all identified as sources of COEs (reviewed by Harrison et al. 2011).

For example, birds in better condition during non-breeding periods may devote more time to foraging or finding resources, which may result in higher survival, larger energy reserves, earlier departure, and faster migration to secure high quality territories, thereby enabling earlier breeding with higher potential success (Marra et al. 1998). Examples of COEs that influence various determinants of fitness (i.e. reproductive success, timing of migration and breeding, recruitment or survival) include prior reproductive effort and timing (Inger et al. 2010), pre-breeding body condition (Cook et al. 2004), migration distance (Bearhop et al. 2004, Schamber et al. 2012), disturbance during migration (Legagneux et al. 2012, Juillet et al. 2012), food availability during the non-breeding season (Bridge et al. 2010), and climate (Harrision et al. 2013). Habitat quality also influences future fitness where individuals occupying low quality habitats in winter showed later departure dates, reduced reproductive success, and lower return rates to wintering grounds compared to birds originating from high quality wintering habitats (Marra et al. 1998, Gunnarsson et al. 2005). Importantly, COEs are not a specific phenomenon in and of themselves, but rather a pathway for various mechanistic drivers (see above) to alter an individual's state and generate variation in fitness.

1.2 Conservation Rationale

The Prairie Pothole Region (PPR) of North America is one of the continent's most productive waterfowl breeding regions, with high densities of glacial depression wetlands and remnant grasslands providing critical nesting and brood rearing habitat for ducks (Prairie Habitat Joint Venture 2008). Yet, these same are some of the most highly modified landscapes on earth,

where an estimated 40-70% of wetlands in the PPR have been lost to agricultural development due to agricultural intensification over the past century (Government of Canada 1996, Gauthier et al. 2003, Gage et al. 2016).The continued conversion of habitats poses a serious threat to not only retention of native grassland habitat but the long-term security of highly productive seasonal and temporary wetlands and associated breeding habitat for many bird species (Horn et al. 2005, Dahl and Watmough 2007). Consequently, grassland birds, including many waterfowl species that breed in the PPR, must inevitably settle in highly modified landscapes, contributing to population declines (Stanton et al. 2018). Understanding the influences of these modified landscapes on avian population dynamics is a vital piece of information for waterfowl management and habitat conservation.

Northern pintails (*Anas acuta*), a grassland bird that breeds within the PPR, have exhibited population declines in recent decades. Pintails typically exhibited "boom or bust" reproductive cycles aligned with prairie wetland conditions, but that pattern weakened during the 1990s despite abundant prairie wetlands (Miller and Duncan 1999). By 1991, pintail populations declined an estimated 67% from a high of 5.6 million birds in the 1970s to only 1.8 million birds, and recently despite suitable water conditions, the current population estimate of 2.4 million in 2018 is still 40% below the long-term average and North American conservation goals (NAWMP 2004, USFWS 2018). The chronically low population and lack of recovery has been hypothesized to result from low recruitment due to low nesting success and/or poor duckling survival (Miller and Duncan, 1999). Several studies have evaluated nesting success in diverse landscapes (Greenwood et al. 1995, Klett et al. 1988), whereas few have documented duckling survival and fledging success in the PPR; likewise, there has been limited contrast of pintail breeding success between agriculturally modified landscapes typical of the modern prairies and the native grasslands where pintails evolved. Investigation of prairie land use and landscape influences on pintail duckling survival was identified as a priority research need by an international team of waterfowl scientists in 2001 (Miller et al. 2003).

Ducks Unlimited Canada's (DUC) Pintail Initiative has started to make substantial investments into programs to benefit pintails. Thus, understanding the drivers of pintail decline will enable more effective implementation of management and mitigation measures. Recently, fall-seeded cereal crops like winter wheat have been strongly promoted to increase waterfowl nesting success in agricultural areas (Devries et al. 2008a, Skone et al. 2016) but the potential

benefits for duckling survival are unknown. If landscape-level drivers influence duckling survival in agricultural areas as suggested in previous literature (Peterson et al. 1999, Guyn and Clark 1999, Amundson et al. 2011, Bloom et al. 2012) then benefits of higher nesting success in fall-seeded crops may not be fully realized. Additionally, understanding how additional mechanisms interact with the environment and influence reproductive success in both pintails and other species not exhibiting population level declines enables consideration of not only the drivers of productivity but may reveal additional avenues for management and conservation action.

1.3 Research Objectives and Thesis Organization

The primary objective of this research is to evaluate contributing factors which influence avian reproductive success across multiple scales. I aim to improve understanding of interactive effects of environment and individual traits as determinants of annual reproductive success. A second objective is to consider whether antecedent events occurring outside of the breeding season influence reproductive outcomes. This dissertation examines both known and hypothesized sources of variation in offspring survival for prairie-nesting ducks in the PPR, and explores hypotheses and predictions based on life history theory, landscape ecology and prior studies of other migratory species.

Specifically, I use a combination of both fine-scale physiologic and large-scale observational data derived from a captive experiment, field studies and existing long-term datasets of waterfowl reproductive success across the Prairie Pothole Region. I begin my evaluation at the intra-individual scale, link fine-scale measures of physiology with intrinsic condition and quality then move to the individual-scale to test for maternal effects. I subsequently evaluate extrinsic influences of landscape composition and configuration by scaling upwards from local environments to regional and even continental influences. I also frame comparisons across landscape gradients between grassland and wetland dominance to help identify consequences of landscape modification. Lastly, intertwined in this investigation are temporal relationships as a third scale, where I consider not only effects from the current season but potential COEs from the previous months and years (Figure 1.1). Assessing the mechanisms by which COEs develop across the annual cycle in migratory birds will improve our

interpretation and understanding of their long-term effects on population processes, allowing for more informed conservation efforts aimed at improving reproductive success.

I have organized this dissertation as multiple manuscripts that bridge across scales to investigate influences on reproductive performance. Several variables and datasets are consistent across scales (and Chapters) while others are addressed specifically within one Chapter to test specific hypotheses. Thus, there is some redundancy in the introduction, description of study sites, and methods between some Chapters.

In Chapter 2, I examine the role that physiology plays to inform our interpretations of intrinsic condition and detection of carry-over effects. I directly test whether a positive relationship exists between allostatic load and feather corticosterone; a key assumption for the interpretation of feather biomarkers that has not been previously examined. I use data from an experimental manipulation of allostatic load for captive mallard ducklings relate patterns in allostatic load (body mass and energetic expenditure) to levels of corticosterone in feathers. I then perform a cross-over experiment to examine whether past or current energetic expenditure and allostatic load drive patterns in feather corticosterone. This will enable me to address a key knowledge gap for the interpretation of carry-over effects using feather corticosterone here and elsewhere.

In Chapter 3, I extend the examination of potential physiological carry-over effects across space and time. I consider whether patterns in feather corticosterone reflect broad regional differences between locations of feather growth and if past antecedent conditions influence future intrinsic condition. I use a combination of isotopic signatures of wing and body feathers, known patterns in continental precipitation, and band-recovery data from hunter-harvested pintails across North America to assign likely feather-origins for prairie nesting pintails. I then compare patterns in isotopic signature between various potential wintering and summer locations and assess if these likely origins have downstream effects on future intrinsic condition. This Chapter integrates both temporal and geographic scales to further understanding of sources of variation in feather corticosterone and its potential carry-over effects.

In Chapter 4, I focus on how intrinsic qualities such as behavior, age, timing of breeding and condition influence reproductive performance and specifically duckling survival. I use reproductive data collected from breeding pintails captured during nesting and monitored

throughout the brood-rearing period in southern Saskatchewan between 2011 and 2012. I consider maternal traits that are known to influence duckling survival in other regions and species, as well as hypothesized relationships within an index of female behaviour, a trait not examined in the literature to date.

In Chapter 5, I extend the investigations from Chapter 4 to examine how the composition and configuration of the environment influence duckling survival across multiple spatial scales. I combine information on duckling survival, habitat use, brood movement and weather in areas with a sharp landscape gradient, ranging from areas of intensive crop production (with a high incidence of fall-seeded crops) to large tracts of native prairie and forage grasslands. Pintail survival and habitat relationships are compared between grassland-dominated landscapes – presumed to be more characteristic of the pintail's ecological niche – and cropland-dominated landscapes that represent the current broad-scale conditions on the Canadian PPR. I first test for differences between landscapes, then consider a management relevant scale and test hypothesized relationships between nesting habitat composition and duckling survival, and specifically examine how the management strategy of planting winter wheat may influence duckling survival in cropland landscapes. I then consider how the local composition and configuration of habitats immediately surrounding the brood influence its survival. This enables me to consider not both the broad patterns that may be a result of anthropogenic change in context of other regional factors as well as the proximate drivers that can inform conservation strategies and targeted management action.

In Chapter 6, I use multiple datasets gathered from across the PPR to test for relationships between intrinsic and extrinsic factors known or hypothesized to influence reproductive performance in prairie nesting waterfowl. I first examine whether variation in measures of corticosterone sequestered in feathers are related to reproductive effort or environmental conditions. I used 9 years of recapture data from St. Denis National Wildlife Area between years 1983 and 2000 (Clark and Schutler 1999, Dzus and Clark 1998, Clark et al. 2005) to determine repeatability of corticosterone measures and identify potential within season contributions that influence those measures. I then examine the relative contributions of intrinsic quality (both past and current) or extrinsic factors of the surrounding landscape that influence mallard reproductive success. I use detailed reproductive information obtained from across the Prairie Parklands during the Prairie Habitat Joint Venture Mallard Assessment (Devries et al. 2008b, Howerter et

al. 2014) between years 1993 to 2000 and test for evidence of hypothesized carry-over effects using feather biomarkers while simultaneously considering known effects from intrinsic conditions at capture and extrinsic effects of landscape composition. Lastly, in Chapter 7, I synthesize my findings in the context of multiple scales and identify avenues for future work and investigation.

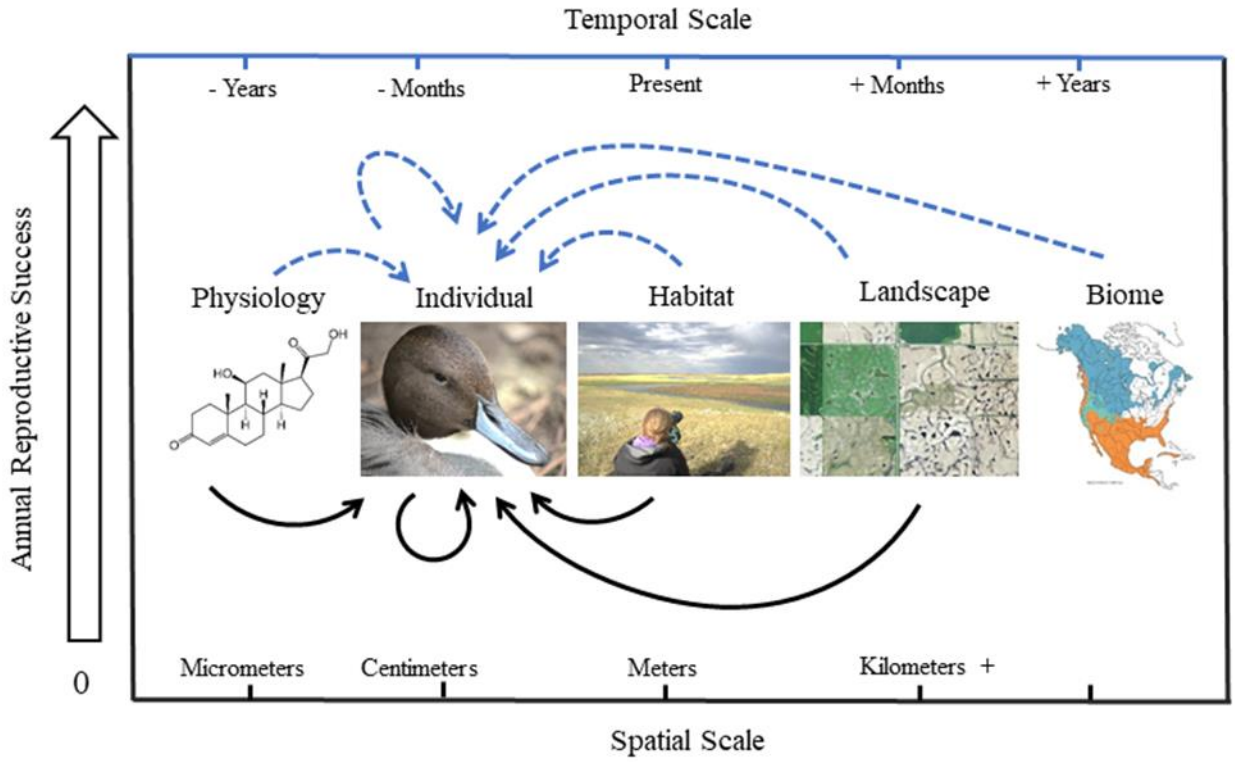

Figure 1.1. Dissertation framework for investigation of intrinsic and extrinsic influences on avian reproductive success across multiple scales ranging from physiology, individuals, habitats, landscapes and biomes. The y-axis represents increasing reproductive success by which each category contributes. The lower x-axis represents multiple spatial scales, ranging from intra-individual to habitats and biomes. The upper x-axis represents investigating across temporal scales and consideration of both past and current effects. Arrows represent investigation of its corresponding influence on individual reproductive success relative to each scale (temporal = dash; spatial = solid).

CHAPTER 2. DOES FEATHER CORTICOSTERONE REFLECT ENERGETIC EXPENDITURE AND ALLOSTATIC OVERLOAD IN CAPTIVE WATERFOWL?

While I use the pronoun "I" throughout this chapter I would like to acknowledge the contributions of coauthors and reviewers. This was reprinted from: Johns, D. W., T. A. Marchant, G. D. Fairhurst, J. R. Speakman, and R. G. Clark. 2017. Biomarker of burden: Feather Corticosterone reflects energetic expenditure and allostatic overload in captive waterfowl. Functional Ecology 32:345-357, with permission from © 2017 British Ecological Society.

2.1 Introduction

Allostasis, or the act of achieving stability through change, maintains internal homeostasis through adjustable physiological set-points that depend on the current environment or life cycle stage (McEwan and Wingfield 2003, McEwan and Wingfield 2010). Using energy as the main currency, the allostasis model attempts to explain how individuals respond to energetic demands and predicts how changes in individual condition or state may develop as a result of imbalances between individual energy requirements and energy available within the environment. The total energetic requirements of an individual, termed allostatic load (McEwan and Wingfield 2003), consists of energy needed for baseline function, predictable events such as daily routines and periods with increased demand (e.g. breeding, migration, or moult). Unpredictable events (i.e. storms, stressors, etc.) impose additional burdens on allostatic load in an additive manner.

Energy-regulating hormones such as glucocorticoids are central to allostasis because they modulate shifts in physiologic response necessary to adapt to fluctuating allostatic loads. Glucocorticoids are released by the hypothalamic-pituitary-adrenal (HPA) axis and, under low allostatic loads, facilitate metabolic function through regulation of blood glucose levels and promotion of foraging behaviours (Landys et al. 2006, Romero and Butler 2007, Busch and Hayward 2009). These short-term elevations in glucocorticoid can be adaptive and enhance fitness during specific periods and life cycle stages such as reproduction (Bonier et al. 2009a, Bonier et al. 2009b, Crespi et al. 2013). During periods of high allostatic load in birds, the hormone corticosterone (CORT) is secreted in greater concentrations, promoting protein catabolism, gluconeogenesis and lipid mobilization (Landys et al. 2006, Romero and Wingfield

2015). When allostatic load exceeds an individual's energy intake, or elevated allostatic loads are sustained for extended periods despite an abundance of available energy, a state of allostatic overload may be triggered. During such periods, the associated elevation in CORT can degrade individual state to cope with (i.e., pay for) energy deficits, resulting in reductions in body mass, immune function, growth or suppression of non-essential behaviours (McEwan and Wingfield 2003, Landys et al. 2006, Romero and Butler 2007, Blas 2015) that can ultimately influence individual quality (Angelier et al. 2010), and reproduction (Blas et al. 2007, Gouette et al. 2010, Done et al. 2011). Therefore, energetic context is an important consideration for ecophysiological studies (Madliger and Love 2013).

Baseline measurements of CORT are typically obtained from plasma which must be collected immediately upon capture, an important consideration for studies of wild animals and periods where animal location is not predictable (Sheriff et al. 2011). In birds, CORT is incorporated into feather tissue (hereafter, $CORT_f$) by diffusion through the blood quill during feather growth (Jenni-Eiermann et al. 2015). $CORT_f$ represents a record of both baseline and acute responses during the period of feather growth, ranging from days to weeks, that persists until feather replacement (Bortolotti et al. 2008, Bortolotti et al. 2009, Lattin et al. 2011, Fairhurst et al. 2013a, Jenni-Eiermann et al. 2015). Several studies have used $CORT_f$ to investigate diverse ecological questions including relationships with foraging effort, behaviour, survival, reproductive success and investment, as well as the quality of both individuals and environments (reviewed by Romero and Fairhurst 2016).

To properly interpret $CORT_f$, it is necessary to understand the factors driving its variation (Romero and Fairhurst 2016). Previous studies have postulated that patterns of $CORT_f$ are driven by changes in energetic expenditure, demand or management (Fairhurst et al. 2012, Crossin et al. 2013, Legagneux et al. 2013, Fairhurst et al. 2015, Harms et al. 2015, López-Jiménez et al. 2015, Pérez et al. 2016). Yet despite the establishment of relationships between energetic expenditure and CORT levels in plasma (McEwan and Wingfield 2003, Landys et al. 2006), little work has been conducted to validate the relationship between energetic expenditure and $CORT_f$ (Romero and Fairhurst, 2016). This has hampered the ability to use $CORT_f$ as a biomarker of allostatic load in ecological contexts (Romero and Fairhurst, 2016), and particularly for studying carry-over effects (COEs) that operate across life cycle stages (sensu Norris 2005, Norris and Marra 2007, Harrison et al. 2011).

Recent studies of COEs using $CORT_f$ from post-breeding or wintering periods have found important relationships with subsequent individual condition, breeding performance and investment (Crossin et al. 2013, Kouwenberg et al. 2013, Harms et al. 2015, Boves et al. 2016, Latta et al. 2016, Pérez et al. 2016). However, results have not been consistent (Legagneux et al. 2013, Bourgeon et al. 2014), possibly because prior history of energetic demands, which is unknown in many studies, may influence future $CORT_f$ values (e.g. Aharon-Rotman et al. 2017). If $CORT_f$ responds to both current and past allostatic load, then studies using $CORT_f$ to address questions about the effects of energy demand on COEs could be ambiguous.

Thus, my objectives were to determine experimentally the extent to which $CORT_f$ reflects allostatic load during feather growth and is influenced by past energetic conditions. I examined **1)** whether increased workloads and energetic demand alter allostatic load, individual condition and $CORT_f$, and **2)** if $CORT_f$ response is influenced by energetic demands during and/or before feather growth. I hypothesized that **H1)** experimental increases to daily workload (i.e., energetic costs of daily routine) would increase energy expenditure and allostatic load, which would then be reflected in elevations of $CORT_f$ from growing feathers and a suppression of growth and body mass, and **H2**) $CORT_f$ would reflect energy demands during feather growth such that individuals exposed to the greatest total energy demands across multiple moults would possess the highest levels of $CORT_f$. Alternatively, if corticosterone secretion does not reflect energetic demand or allostatic load, then I expected that $CORT_f$ would be similar between individuals, regardless of workload.

2.2 Materials and Experimental Design

2.2.1 Animals and Housing

One-day-old female mallard (*Anas platyrhynchos*) ducklings (N = 123), obtained from a commercial game-bird hatchery (Metzer Farms, Gonzales, CA, USA), were loose-housed at the University of Saskatchewan, Canada. Two rooms of ~15 m^2 were each divided in half (i.e., making four "pens") using opaque polyethylene panels to prevent visual contact. Each pen had sources of food, water, and heat lamps placed in proximity. All pens received *ad libitum* food (Whole Earth poultry starter, Saskatoon, SK, CAN) and water via poultry feeders (polyvinyl chloride pipe) and commercial waterers, respectively. As ducklings aged (> 14 days) heat lamps were removed and replaced waterers with water basins (dimensions: 1.5 m wide by 0.3 m depth)

for a continuous supply of fresh water for drinking and swimming. Room temperature was maintained at 24°C for the first 3 weeks and lowered to 20°C thereafter with lighting following local astrologic cycle. Following a 9-day acclimation period, ducklings were weighed, marked with individually identifiable web-tags (Alliston 1975), and randomly assigned to rooms and treatment groups. Additionally, following adequate leg development (ca. 21 days) I used metal leg-bands and colored plastic cable ties to aid in identification.

2.2.2 Workload Manipulations and Experimental Setup

I experimentally increased daily workloads using elevated towers and/or weighted backpacks. Tower treatment (T) pens had feeders placed on adjustable-height wooden towers (dimensions: 1.2 m tall by 0.5 m long by 1.0 m wide; see Figure A.1 in Appendix A). Access to the feeder was gained via a 1.5 m long ramp extending from the top of the tower. To increase the effort required to access food, feeders were suspended away from the tower ledge, positioned just above the top of a second steeper ramp covered with polyethylene (i.e., a slide). Feeding birds were required to perch near the edge of the platform and would be forced down the slide due to either: i) a loss of balance or ii) being pushed by other birds accessing food; birds then had to re-climb the tower to resume feeding. As captive ducks prefer to consume food with water, waterers were placed on the opposite side of the pen at ground level, again forcing feeding birds to return to ground level and traverse the pen's length to drink. To maintain work effort as ducklings developed, towers were raised every 2 days from ground level, reaching a final height (1.0 m; ramp slope, 42°) on day 10. Additionally, wooden obstacles (dimensions: 121 cm long by 10 cm wide by 5 cm tall) were placed perpendicular to the travel route to increase workload of birds as they moved between food and water. Obstacles were added semi-weekly by increasing the number or height of the obstacles. Control treatment (C) pens had both food and water at ground level. As environmental enrichment can influence $CORT_f$ levels in captive birds (Fairhurst et al. 2011) I placed structures mimicking towers, ramps and obstacles in control pens to provide equal space and configuration, but which were inaccessible to birds and did not inhibit movement between food and water (Figure A.1).

Weight treatment (w) consisted of weighted backpacks with an adjustable harness (Figure A.1). Backpacks (dimensions: 5 cm by 6 cm) were made from 2 mm neoprene (Brooks Wetsuits Ltd., Vancouver, BC, CAN) and secured using hot melt adhesive. Harnesses were adapted based on designs for small-bodied waterfowl (Roshier and Asmus 2009) but modified to facilitate

adjustment as the bird grew. Teflon ribbon was replaced with clothing elastic (6.4 mm) during the period of rapid growth (days 21 – 57) and polyester ribbon (10 mm; days 95 – 133) to minimize wear and friction when birds were fully grown. Straps were passed through small holes in the neoprene backpack, adjusted for proper fit, secured with metal safety pins which were then covered by a neoprene flap. Harnesses could be expanded or tightened by moving the safety pins up or down the securing straps with excess harness material placed inside the pouch. Backpacks were loaded with pre-measured lead weights based on current bird body mass. Loads (including harness and pack material) were targeted for 10 – 12% of body mass when ducklings were 21 – 28 days old and 15 – 18% of body mass for the remainder of the experiment. Backpack loads were targeted based on published studies investigating energetics in load-carrying waterfowl (Tickle et al. 2010, Tickle et al. 2013). Harness fit and backpack weights were adjusted weekly during phase one (see below) and every 2 weeks during phase two to accommodate changes in body mass. To control for potential handling effects on $CORT_f$ in birds carrying backpacks (Cw/Tw), I captured and handled all non-weighted birds (Cc/Tc) equally during harness adjustment periods.

Experiments were conducted in two separate phases, each approximately 6 weeks in length with a 5-week intermission (phase one: Sept. – Oct. 2014, phase two: Nov. 2014 – Jan. 2015; Figure 2.1). I used a repeated measures design with two nested treatments: a tower treatment (T), tower control (C), and a nested weight treatment (w) and weight control (c) which created four treatment groups (Tw, Tc, Cw, Cc). The experimental setup was replicated in both rooms and all treatment groups were represented in each room.

2.2.3 Phase One

Workload treatments were initiated progressively (day 9, food and water separated; day 13, towers raised; day 15, obstacles added; day 21, weighted backpacks applied), and weighed birds (nearest 10 g with a Pesola spring scale) biweekly during days 9 – 24 and weekly thereafter (days 25 – 57), as indicated in the detailed sampling schedule (Figure 2.1). I estimated daily energy expenditure (DEE) at the start of wing feather growth (day 24) using doubly labelled water (DLW; Lifson and McClintock 1966, Speakman 1997, Butler et al. 2004; see below for analytical procedure). Doubly labeled water consists of trace isotopes of hydrogen and oxygen and when administered to an individual are dissipated at different rates from the body. Serial sampling enables the estimation of CO_2 production and energy expenditure. I randomly selected

DLW birds (N = 17 total) from both experimental rooms but targeted treatment groups predicted to show the greatest contrast in DEE (i.e., Cc and Tw). Birds were weighed and then injected intraperitoneally with 0.56 mL DLW containing 66.6 atom percent excess (APE) oxygen-18 (^{18}O) and 34.98 APE deuterium (^{2}H). A single bird showed signs of DLW leakage post–injection and was excluded from analysis. Birds were placed in a cloth bag for 60 min to allow DLW to reach equilibrium with body water in injected birds. Prior to release a blood sample (200 µL) was collected from the jugular vein to estimate initial isotope enrichment. Blood samples were immediately transferred into several 50 µL non-heparinized glass micro-capillaries tubes and flame-sealed until analysis by mass spectrometry. In addition, I collected blood samples from five unlabeled ducklings to determine mean background isotope levels. All DLW-injected birds were recaptured after 48 h (mean 48.1 h ± 0.5 SD) to minimize circadian influences (Speakman and Racey 1988). Upon re-capture, birds were re-weighed, and a second blood sample was taken as described above to estimate final enrichment of isotopes. To conform with animal care space limits, total sample size was reduced on day 37 (*N = 100*) using random selection. With completion of wing feather growth (day 57), three greater secondary covert (GSC) feathers from one wing were collected from each bird, placed in paper envelopes, and stored at room temperature until $CORT_f$ analysis (below).

2.2.4 Rest and Moult

Immediately following feather collection, birds were weighed and had primary wing feathers clipped from the right wing to prevent flight and minimize injury potential. I lowered towers, and removed all obstacles, backpacks, and pen dividers from each room, thereby allowing birds to intermix for up to 4 weeks. In preparation for phase two I randomly selected a smaller set of birds (N = 80) to undergo feather moult. Moult was induced through photoperiodic adjustment from astrologic time (~ 15 h light) to total darkness (day 82) and the removal of food for 3 days, followed by an increase to a 12 h light cycle (Corey and Peralta 2015). To ensure all birds would initiate moult simultaneously I also pulled four GSC feathers from one wing (day 85).

2.2.5 Phase Two

To test for carry-over effects of past energetic demand on current $CORT_f$, I conducted a cross-over experiment using the same workload treatments as described above. I randomly

assigned birds to rooms and treatments, stratifying by previous treatment. For example, of 20 "Cc" birds from phase one, 5 birds were randomly assigned to each treatment (Cc, Cw, Tc or Tw), resulting in four new groups (Cc-Cc, Cc-Cw, Cc-Tc, and Cc-Tw). These allocations were repeated for the remaining treatment groups, creating 16 combinations. Workload treatments (towers, obstacles, and backpacks) were imposed on birds (according to their treatment) for an additional 7 weeks while GSC feathers were regrown. To minimize handling effects on $CORT_f$, birds were handled on 3 occasions over the 7-week period (days 95, 104, and 133), and then the newly grown GSC feathers were collected (day 133). Birds were re-weighed and measured for head-bill, total tarsus and keel lengths (nearest 0.1 mm with dial calipers).

2.3 Laboratory Analyses

2.3.1 Daily Energy Expenditure (DEE)

Analysis of isotopic enrichment of blood was performed blind by isotope ratio mass spectrometry at the University of Aberdeen, Aberdeen, Scotland, UK. Samples were run alongside three lab standards for each isotope and three International standards to correct delta values to ppm. I used equation 7.17 of Speakman (1997) and a single-pool model to calculate rates of CO_2 production as recommended for use in growing birds or animals < 1 kg in body mass (Speakman 1997, Visser and Schekkerman 1999, Visser et al. 2000). I corrected for a fractional evaporative water loss of 25% and assumed a respiratory quotient (RQ) of 0.80, a value calculated using sea ducks during terrestrial locomotion (Hawkins et al. 2000). Initial body water pool was calculated using ^{18}O-dilution space via the plateau method (Speakman 1997) and final body water pool was determined based on measurement of final body mass assuming constant body water fraction. A subset of birds (N = 4) did not have precise blood sample times but were recorded within 3 min of collection. To determine how DEE would be influenced by variation in collection times I calculated DEE by including or excluding these individuals. I found differences of ± 5 mins in collection time would result in an increase in DEE by ± 1% and found no differences in results based on the inclusion or exclusion of individuals with estimated times (i.e., collection time was not statistically influential). Therefore, DEE estimates are reported for all birds in the analysis.

2.3.2 Feather Corticosterone ($CORT_f$)

I measured levels of $CORT_f$ in all collected GSC feathers following procedures established by Bortolotti et al. (2008). Feather samples were randomized at multiple points during the extraction and assay process. Feathers were measured and weighed with the calamus removed and minced into < 5 mm^2 pieces. I added 10 mL of methanol (HPLC grade, Fisher Scientific, Fair Lawn, NJ, USA) to feather samples, sonicated for 30 min at room temperature then incubated overnight in a 50°C water bath. The methanol extract was separated from feather material through vacuum filtration using a polyester fiber plug. Feather material, sample vial, and filter were washed twice with an additional 5 mL of methanol, which was added to the original extract. Extract methanol solution was left to evaporate under a fume hood for 48 h, and extraction residues were reconstituted in 600 mL of phosphate buffered saline solution (0.05M, pH 7.6) then frozen at -20°C until radioimmunoassay (RIA) using a CORT antibody (Sigma Chemicals, St. Louis, MI, USA, product No. C8784). I assessed extraction efficiency by spiking three additional feather samples with a known amount (ca. 5000 CPM) of [^{3}H] CORT prior to extraction. I conducted two extractions, with a mean (± SD) recovery of 89.8 ± 0.1% of the radioactivity within reconstituted samples. Serial dilutions revealed displacement curves parallel to standard curves. Inter-and intra-assay variability was assessed using the coefficient of variation (CV) of known standards. Samples and standards were run in duplicate across six assays with a mean (± SD) intra-assay CV of 6.6 ± 2.2%, inter-assay CV of 9.4 %, and all samples were above detection limits (ED_{80}) of 18.3 ± 3.4 pg 100 μl^{-1}. As feathers are believed to grow in a time-dependent rather than mass-dependent manner, $CORT_f$ is expressed as concentrations in pg mm^{-1} feather (see Bortolotti et al. 2008, 2009, Bortolotti, 2010, Jenni-Eiermann et al. 2015, Romero and Fairhurst 2016). Wing feathers were slightly smaller in Tw treatment birds (Table A.1; Figure A.2), suggesting potential energetic trade-offs with feather quality (Romero et al. 2005, Desrochers et al. 2009, Lattin et al. 2011). Although $CORT_f$ values were corrected by feather length, the implications for reduced feather quality and how density influences $CORT_f$ are still unknown but worthy of further investigation (Harris et al. 2016, Romero and Fairhurst 2016). Because recovery varied so little between extractions, I did not adjust $CORT_f$ values by recovery efficiency. $CORT_f$ analyses were performed at the University of Saskatchewan, Saskatoon, Saskatchewan.

2.4 Statistical Analysis

I tested for differences between rooms at the start of each experimental phase using analysis of variance (ANOVA) and, unless otherwise indicated, Type II analysis of covariance was used to assess how workload treatments influenced body mass, growth rate, DEE and $CORT_f$ in phase one and how past and current workload influenced body mass and $CORT_f$ in phase two. I also examined if prior $CORT_f$ values in phase one influenced subsequent $CORT_f$ levels in phase two. All $CORT_f$ were log transformed values to improve normality and ensure model residuals were normally distributed. I used stepwise removal of non-significant terms to determine final models of important main effects and used an alpha level of 0.05 for all statistical tests. Means and standard error are reported in text and figures. All analyses were conducted within R statistical software v. 3.2.1 (R Development Core team 2015).

2.4.1 Phase One: Treatment Effects on Growth, Energy Expenditure, and $CORT_f$

Duckling body mass did not differ between rooms (ANOVA: $F_{1,117} = 0.11$, $P = 0.75$) or treatment groups ($F_{3,117} = 1.63$, $P = 0.19$) following initial random assignment. However, unequal feedings between rooms on days 11 and 12 did delay body mass gain by day 13 ($F_{1,117} = 20.25$, $P < 0.01$). As I was primarily interested in treatment effects, body mass was corrected for differences between rooms by subtracting mean body mass for each room from individual measurements of mass (i.e., relative body mass). I then examined if relative body mass at the time of feather collection (response variable: day 57) was influenced by workload treatments (categorical: Cc, Cw, Tc, Tw), initial body mass (covariate: day 9) and its interaction. To determine if duckling growth rates differed between treatment groups, linear regression was used to calculate the growth slope for individual ducklings during the period of rapid body mass gain (13 – 43 days) and standardized individual growth rates based on room-specific averages. I then modeled relative growth rate (response variable) in relation to workload treatment and initial body mass.

To test the assumption that DEE was influenced by workload treatment, I examined if the combined workloads (Tw) increased estimates of DEE (response) at the start of wing feather growth (day 24). As estimates of DEE are contingent on body mass, I included mean body mass for each bird over the 48 h post-injection period as a covariate, in addition to main effects of workload treatment (categorical; two levels: Cc vs. Tw). I used analysis of covariance to determine if the concentration of $CORT_f$ in wing GSC feathers varied due between treatment groups and a *post-hoc* Tukey's test to examine differences in $CORT_f$ between groups. I found no

support for a difference between rooms for DEE ($F_{1,12} = 1.30$, $P = 0.28$) or $CORT_f$ ($F_{1,93} = 9.15$, $P = 0.82$) and removed that term from consideration for each of the respective models.

2.4.2 Phase Two: Treatment and Carry-over Effects on Body Mass and $CORT_f$

To facilitate comparison, I used an approach similar to phase one and examined how final body mass (response; day 133) differed as a function of past workload (i.e., workload treatment from phase one) and current workload (i.e., workload treatment from phase two) as well as the interaction between past and current workloads, when controlling for body mass at the start of phase two (day 95). I tested for covariates influencing $CORT_f$ (response) including past workload, current workload, and the interaction between past and current workload. To further examine if there were carry-over effects (COEs) associated with $CORT_f$, I then replicated the previous analysis and substituted past $CORT_f$ (i.e., $CORT_f$ values from phase one) in place of past workload as a main effect and in an interaction with current workload (i.e., workload × past $CORT_f$). As past workload and past $CORT_f$ were confounded, I did not include both terms in the same model. Like phase one I initially tested for room effects but did not find any support in body mass ($F_{1,70} = 1.11$, $P = 0.29$) or $CORT_f$ ($F_{1,67} = 1.09$, $P = 0.30$) and removed that term from further consideration. Lastly, analysis of variance was used to examine if morphology was affected by workload treatment using tarsus, keel and head-bill lengths.

2.5 Results

2.5.1 Phase One

Relative duckling body mass at the time of feather collection (day 57) differed between workload treatments, after controlling for effects of initial body mass (Table 2.1), however I found no support for the interaction ($F_{3,91} = 0.90$, $P = 0.45$). Relative body mass corrected for room effects was lighter for all workload treatments relative to controls, and the combined application of towers and weights resulted in the lightest birds (Figure 2.2A). Relative growth rates differed between treatments (Table 2.1) and were fastest in control birds (Cc: 2.78 ± 0.50 g day^{-1}) relative to single workload groups (Cw: -0.47 ± 0.50 g day^{-1}; Tc: 0.04 ± 0.51 g day^{-1}), with the slowest growth rates expressed in the combined Tw workload treatment birds (-2.35 ± 0.50 g day^{-1}). Growth rates were not significantly related to initial mass ($F_{1,94} = 3.46$, $P = 0.07$). Post-hoc analysis revealed differences among all workload groups except intermediate workload groups Cw and Tc.

Over the 48 h period when I estimated DEE, the average backpack weight (expressed as % body mass) was 9.6 ± 0.2 % and averaged 15.1 ± 0.3 % over the duration of phase one (range: 9 – 19 %). DEE was significantly higher in Tw workload birds compared to Cc birds when controlling for differences in body mass (Table 2.1; Figure 2.2B). Workload treatments significantly increased the amount of $CORT_f$ measured in wing feathers (Table 2.1). *Post-hoc* comparisons between workload combinations revealed that $CORT_f$ values were lowest in control birds compared to single workload groups or the combined workload birds, however no differences were found among the three workload treatment groups (Figure 2.2C). Final model variables and test statistics for phase one can be found in Table 2.1.

2.5.2 Rest and Moult

During the 4-week removal of workload treatments, body mass increased in all groups but declined on average 41 ± 6 g during the induced moult due to fasting for 72 h. During phase two, no body mass differences were found between treatment groups either prior to ($_{ANOVA}$ day 82; $F_{3,95} = 1.48$, $P = 0.22$) or immediately following (day 95; $F_{3,76} = 0.84$, $P = 0.48$) moult, suggesting that the effect of fasting was short-lived (Figure 2.1).

2.5.3 Phase Two

After 7 weeks of exposure to a second round of workload treatments I found significant effects of phase two workload treatments on body mass after controlling for effects of initial body mass (Table 2.1). As predicted, body mass was greatest in control (Cc) ducks and declined with workload treatment and was lowest in birds carrying loads over obstacles (Figure 2.3A). I found no support for differences in mass explained by phase one workload ($F_{3,68} = 0.65$, $P = 0.58$) or an interaction between past and current workload ($F_{9,59} = 0.61$, $P = 0.79$).

Examining whether past workloads or physiologic response influenced current $CORT_f$ levels (i.e. COEs), I found that $CORT_f$ levels in re-grown feathers during phase two were related to current workload treatments and phase one $CORT_f$ levels (Table 2.1). Consistent with phase one, $CORT_f$ values from phase two were lowest in the Cc group, intermediate for Cw and Tc groups and highest in Tw birds, however, differences were only significant between Cc and Tw birds (Figure 2.3B). When I examined whether past physiologic response influenced current $CORT_f$ levels (i.e., COEs), I found significant positive effects of phase one $CORT_f$ levels when controlling for current workload (Figure 2.3C). I found no support for past workload treatments

($F_{3,68} = 0.92$, $P = 0.44$), or its interaction with current workload ($F_{9,59} = 0.91$, $P = 0.53$); likewise a similar interaction between past $CORT_f$ levels and current workload was also not influential ($F_{3,67} = 2.19$, $P = 0.10$). I found no significant differences in structural size (tarsus, keel or head-bill length) between workload treatment groups at the completion of phase two ($P > 0.11$). Final model variables and test statistics for phase two can be found in Table 2.1.

2.6 Discussion

Direct linkages between fitness metrics and the avian biomarker of feather corticosterone ($CORT_f$) have typically been predicated on the untested assumption that elevations in $CORT_f$ reflect responses to energetic challenges. However, to date most studies using $CORT_f$ have largely been correlative, creating a need for experimental evidence examining relationships with energetic demand (Romero and Fairhurst 2016). Additionally, use of $CORT_f$ as a retrospective biomarker relies upon improved understanding of the interplay between individual ecophysiology and conditions during feather growth. To my knowledge, this is the first study to directly address both these knowledge gaps by experimental manipulation of energy expenditure and allostatic load during feather growth.

Birds that experienced higher daily workloads by traversing obstacles, climbing towers, and/or carrying additional weight for multiple weeks had lower body mass, slower growth rates and, as predicted, higher DEE and $CORT_f$ levels. I also assessed the influence of carry-over effects (COEs) in $CORT_f$ levels and show that $CORT_f$ reflects current energetic demands during feather replacement but in some cases is also influenced by antecedent glucocorticoid levels in juvenile waterfowl. Collectively, these results provide a critical validation of the allostatic nature of $CORT_f$ in response to energetic demand during the period of feather growth and its ability to facilitate detection of allostatic overload conditions.

2.6.1 Body Mass and Growth

This experiment confirmed negative relationships between increased workload (i.e., experimentally manipulated cost of movement) and both body mass and growth rate for precocial birds early in life (Table 2.1, Figure 2.2A), giving us confidence that allostatic load was elevated to an overload state due to increased workload and energy demands. McEwan and Wingfield (2003) describe allostatic load as consisting of the cumulative energetic requirements for basic homeostasis (Ee), plus energy required to find, process and assimilate food under ideal

conditions (Ei), and the energy required to fulfill daily routines under non-ideal conditions (Eo). The impact of increases to allostatic load (Ee + Ei + Eo) is determined by the amount of energy available in the environment (Eg). Type I allostatic overload occurs when perturbations elevate Eo and energy demand exceeds availability (Ee + Ei + Eo > Eg), creating a negative energy balance and triggering glucocorticoid response. Type II allostatic overload occurs when energy availability is not limiting (Ee + Ei + Eo < Eg) and the elevation of Eo and allostatic load occurs over extended periods, resulting in chronic elevations of glucocorticoid hormones which may lead to pathological effects (McEwan and Wingfield 2003, Wingfield 2005, McEwan and Wingfield 2010, Blas 2015). In this experiment, birds were forced to endure extended elevations in energy demand, resulting in Type II allostatic overload as birds had access to unlimited food (McEwan and Wingfield 2003, Wingfield 2005, McEwan and Wingfield 2010).

Previous studies have linked increases in both exogenous and endogenous CORT in birds to inhibition of growth, development, body condition and structural size (Lin et al. 2006, Hull et al. 2007, Müller et al. 2009, Schultner et al. 2012, Durant et al. 2013). Experimental manipulations of workloads in birds have increased levels of CORT and decreased body mass (Bonier et al.2011, Rivers et al. 2017 but see Leclaire et al. 2011). Lodjak et al. (2015) found that levels of $CORT_f$ were influenced by growth conditions and nestlings raised in what was interpreted as poorer quality habitats had reduced body mass and higher levels of $CORT_f$ compared to nestlings from superior habitats. Results are consistent with these findings, suggesting that unexpected but long term increases in energy expenditure elevated allostatic load, which promoted the release of CORT (reflected in $CORT_f$) and led to Type II allostatic overload, with negative effects on body mass, growth rate, and body size. However, I found that mallards regained body mass when relieved of increased workloads, similar to results found in nestling kestrels (Müller et al. 2009). Morphometric measurements of head-bill, keel, and tarsus length showed no differences between treatment groups at maturity, suggesting that Type II allostatic overload conditions were transitory, allowing ducklings to recover body mass and resume growth when the energetic burden was removed.

2.6.2 Daily Energy Expenditure

The additional burden of carrying weights over obstacles increased DEE in juvenile mallards by approximately 7.2 % when controlling for body mass. Over a 48 h period, Tw birds had slightly less than proportional increases in DEE in relation to carried load, as reported in

previous studies (McGowan et al. 2006; Tickle et al. 2013; but see Tickle et al. 2010). Differences in load-carrying efficiencies of mallards in this experiment compared to previous studies are likely a methodological consequence of measuring DEE over an extended period and experimental design. Compared to shorter duration treadmill studies with fixed lengths of exposure, this experiment examined continuous workload over multiple weeks and relied upon daily movements to induce energetic costs. Extended periods of work may force birds to adapt or become trained, thereby dampening the effects of increased exertion, or adjustments in behaviour (reduced activity) may offset impacts on DEE. Handicapped birds can reduce activity levels to compensate for increases in effort of movement (Deerenberg et al. 1998, Elliot et al. 2014) as in natural studies of bird migration (Guillemette et al. 2012). I did not measure DEE in all treatment groups and cannot be certain that obstacles and towers (Tc) or weights (Cw) alone increased DEE. However, because body mass, growth rate, and $CORT_f$ responded to treatments, it is likely that all workload treatments increased DEE relative to controls, though this study was not designed to differentiate to what degree.

2.6.3 Feather Corticosterone and Allostatic Load

A positive relationship between allostatic load and $CORT_f$ was confirmed. Patterns in $CORT_f$ were opposite to those visible in body mass, growth rate and DEE of mallard ducklings (Figs. 2.3 and 2.4), increasing my confidence that $CORT_f$ was responding to allostatic load. Birds exposed to workload treatments had higher $CORT_f$ levels relative to unburdened birds (Cc), with the greatest differences in birds forced to carry weights over obstacles (Tw). During the second phase of the experiment, levels of $CORT_f$ in wing feathers were reflective of only current workload rather than past demand, albeit at reduced levels compared to phase one. Although body mass loss during phase two mirrored results from phase one, differences in $CORT_f$ were only detected between the most extreme groups (Cc and Tw). Energetic demands faced by Tw birds during phase two likely required sustained elevation of endocrine response, potentially increasing endocrine response attenuation and easier entry into an overload state (Romero et al. 2009, Wingfield 2005, Blas 2015), whereas other workloads (Cc, Cw, and Tc) may not have been sufficient to create allostatic overload conditions, resulting in comparable $CORT_f$ levels.

If workload treatment progressively increased energy expenditure (as suggested by body mass and growth data), then why did I not detect differences among all workload treatment groups using $CORT_f$ in both phases? Exercised ducks can show diminished corticosterone

response from habituation following repeated periods of daily exercise (Harvey and Phillips 1982, Rees et al. 1983, 1985), so repeated exposure to workload treatments may have habituated and thus reduced CORT response to workload treatments over the duration of the experiment. While monitoring HPA function and physiologic mediators of CORT response to the repeated elevation in allostatic load was beyond the scope of this study, I believe that valuable insight could be gained by incorporating such measures in future studies. For example, investigations of how repeated cycles of exposure to, and relief from, energetic burdens impacts the strength of future glucocorticoid response (i.e., wear and tear; Romero et al. 2009) and measures of $CORT_f$ would be highly valued.

It is possible that individual behaviour was influential. During perturbations, birds can change behaviour to shift energy balances and avoid allostatic overload (McEwan and Wingfield 2003, Landys et al. 2006, Blas 2015). For example, seabirds subjected to handicaps (carrying transmitters) decreased activity levels (Elliot et al. 2014), and finches reduced nocturnal activity in response to forced increases in workload (Deerenberg et al. 1998). I was unable to measure activity levels between treatment groups but did note that when some birds were feeding on elevated platforms, others remained at ground level to eat spilled food, temporarily avoiding costs of climbing obstacles and towers (DWJ, pers. obs.). Birds were likely unable to meet the entire daily energetic demands on cost-free food alone (e.g. spilled food was removed daily), these "cheater" birds in tower pens may have partially offset some of the costs associated with the towers or carried weights by feeding at the base of the tower with reduced effort, thereby minimizing allostatic load in spite of workload treatment. Therefore, if birds did compensate for increased energetic demands by reducing overall activity levels through physiological or behavioural adjustment (i.e., increased resting or foraging on lower-cost foods) then CORT response may have been weakened and, thus, $CORT_f$ levels lowered.

One strength of this experiment is the controlled setting and comparison between birds of the same age, sex and life history stage. However, the lack of clear difference between treatment groups in $CORT_f$ levels between experimental phases may be associated with changes in duckling development. Precocial species such as mallards have a well-developed HPA axis and endocrine response early in life (Holmes et al. 1990, Romero and Wingfield 2015), yet other body components like bones, muscles, and feathers must still undergo rapid growth before reaching full development (Starck and Ricklefs 1998). Greater energetic demands during a

period of rapid growth (Ei) may ensure an overall higher allostatic load compared to fully developed adults exposed to the same relative workloads. Similarly, while I attempted to maintain treatment effects by increasing the weight carried and raising obstacle height as birds grew, there is the possibility that towers and backpacks were not as effective at increasing allostatic load and triggering Type II allostatic overload in older ducklings as it was in earlier ages.

Results from this experiment highlight age-related differences in the generalized patterns of energy management influences on $CORT_f$, where effects are manifested differently in young vs. older birds. Such differences have important implications for studies of carry-over effects using $CORT_f$, where younger birds may be more susceptible to overload conditions than older birds and, indeed, such effects may have already been shown (Boves et al. 2016). Researchers should consider how age-related processes may influence energy management for interpretations of differences in $CORT_f$ in wild populations.

Levels of $CORT_f$ are also influenced by environmental enrichment (Fairhurst et al. 2011) and it is possible that the initial application of backpacks and/or adding new obstacles to pens provided unpredictable stimuli which may have increased $CORT_f$ beyond what was expected due to increased efforts of movement during phase one. Although a variety of controls were used to attempt to minimize these enrichment or disturbance effects through the addition of false obstacles, similar handling, and importantly, the complete minimization of handling during phase two. If I assume that enrichment and handling effects were minimized during phase two, then that may explain the lack of treatment group separation and overall lower amount of $CORT_f$ between phase one and two. However, the main relationships and patterns found in phase one are evident in phase two.

2.6.4 Carry-over Effects

I also provide experimental evidence that although inter-individual variation in $CORT_f$ is primarily reflective of current allostatic load during feather growth, antecedent physiologic response does influence subsequent $CORT_f$ levels. After accounting for workload, ducklings with higher levels of $CORT_f$ in wing feathers tended to have higher $CORT_f$ levels in newly regrown feathers. Studies testing for repeatability in measures of $CORT_f$ have found close associations between feathers from the same individual and grown at the same time (Lattin et al.

2011, Aharon-Rotman et al. 2017) and between feather types (Lendvai et al. 2013). Elevated levels of $CORT_f$ in wild sparrows were positively associated with subsequent experimental moults (Aharon-Rotman et al. 2017). Similarly, I found a positive correlation between past and current $CORT_f$ levels, but also controlled for age, gender and moult timing.

Yet, repeatability of endocrine measures found in controlled environments does not appear to be consistent in natural systems (Ouyang et al. 2011, Harris et al. 2016), particularly between years for both individuals and populations (Fairhurst et al. 2013a, Legagneux et al. 2013, see Chapter 6). $CORT_f$ patterns can reflect responses at the local or individual scale (Fairhurst et al. 2013b), which may explain the inconsistent detection or absence of COE effects in the $CORT_f$ literature. The ability for $CORT_f$ to reflect both allostatic load as well as individual variation in physiology leading up to moult, may cloud interpretation of the drivers of $CORT_f$. However, such uncertainty and contrasting results should not suppress the promotion of $CORT_f$ as a biomarker but encourage the future consideration for inter-individual variation in $CORT_f$ and the relative strength of past physiologic response compared to allostatic demand in both controlled and natural settings.

Overall, I verified in an experimental setting that $CORT_f$ responds to energy expenditure and highlight the ability of $CORT_f$ to act as a potential biomarker of allostatic load in waterfowl. My results suggest that the use of $CORT_f$ will facilitate retrospective interpretations of energetic demand that are not possible using other indices such as body mass. Final measures of body mass did not reflect allostatic load during feather growth because ducks showed rapid compensatory growth once workload was reduced. By contrast, patterns of energy management that reflected the sustained elevation of allostatic load and resulted in Type II allostatic overload were registered by $CORT_f$ and occurred prior to Type I overload being triggered.

In a wild setting, if migratory birds were captured upon arriving on breeding grounds, body mass scores might not accurately reflect prior conditions if allostatic load has recovered. However, as $CORT_f$ is retained with the bird until the following moult, feathers can provide retrospective information on overload conditions experienced prior to feather collection (i.e., winter or during migration) which would otherwise be unavailable at the time of capture. I suggest that the use of $CORT_f$ will greatly facilitate retrospective interpretations of adrenocortical function and allostatic load in birds but suggest caution in interpretations of COEs

using $CORT_f$, particularly when sampling across multiple age groups, years or when non-consecutive feathers are collected, and moult timing is unknown. Although these results provide promising insight into how $CORT_f$ reflects energy expenditure and allostatic load, further experimental work and field studies are required to test and validate assumptions of $CORT_f$ in relation to individual energetic demands.

Table 2.1. Final model terms and results assessing the effects of workload treatments on body morphometrics, energy expenditure and feather corticosterone in captive female mallard ducklings.

Phase	Response	Model Terms	F	df	*P* - value
One	BM	Workload	21.07	3,94	< 0.001
		Initial Mass	23.95	1,94	< 0.001
	GR	Workload	17.90	3,95	< 0.001
	DEE	Workload	8.73	1,13	0.010
		Body Mass	84.07	1,13	< 0.001
	$CORT_f$	Workload	9.25	3,94	< 0.001
Two	BM	Workload	15.18	3,71	< 0.001
		Initial Mass	47.33	1,71	< 0.001
	$CORT_f$	Workload	6.70	3,70	< 0.001
		Past $CORT_f$	4.60	1,70	0.036

For each model, I present the F-test statistics, with degrees of freedom (df) and P-values.

Covariates: Body mass (BM; phase one = day 57, phase two = day 133), growth rate (GR; days 13-43), daily energy expenditure (DEE; days 24-26), and feather corticosterone ($CORT_f$; phase one = day 57, phase two = day 133).

Workload indicates the treatment group during the current phase: No workload – Cc, Towers and obstacles-only – Tc, Weights-only – Cw, Towers and weights – Tw. Past $CORT_f$ represents $CORT_f$ values from phase one

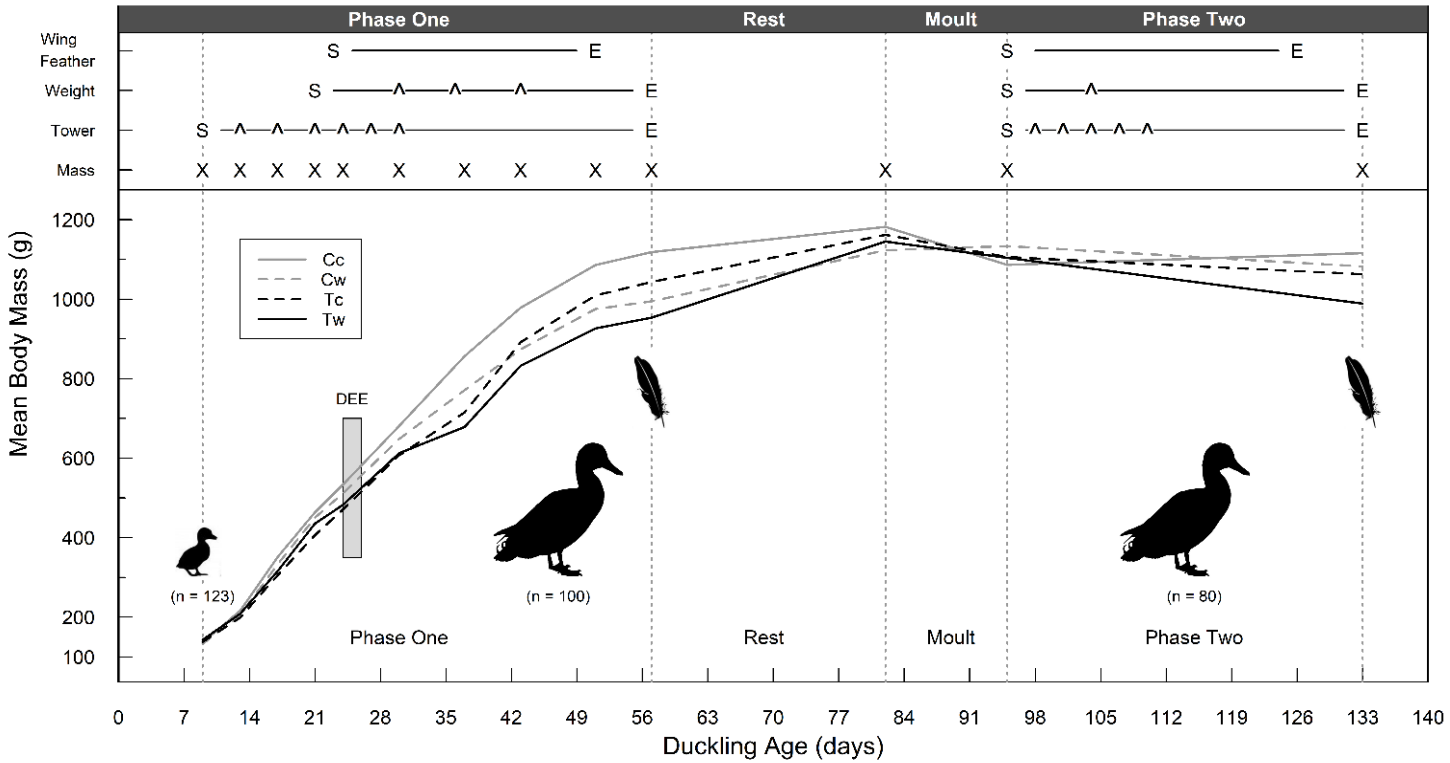

Figure 2.1. Experimental timeline. Top portion: Start (S) and end (E) dates are indicated for wing feather growth and workload treatments (Towers, Weights). Carets (^) indicate manipulation of obstacles, tower height, or carried loads. Dates of sample collection for body mass are indicated with X. Lower portion: Duckling growth (mean body mass; y-axis) in relation to workload treatments and experiment chronology. Duckling age (x-axis) and sample sizes for each experimental phase (dashed vertical lines) are shown. Tower treatment (T-) birds had separation between water and food, elevated on platforms and interspersed with obstacles. Weight treatment birds (-w) carried backpack loads ranging between 15-18% of body mass. Four treatment combinations were created: no towers or weights (Cc; grey solid line), towers only (Tc; grey dotted line), weights only (Cw; black dotted line), and towers and weights (Tw; black solid line). Daily energy expenditure (DEE) was measured over 48 h (grey column) when flight feathers began to emerge. Collection of greater secondary covert feathers (feather symbol) occurred at the end of each phase (days 57 and 133).

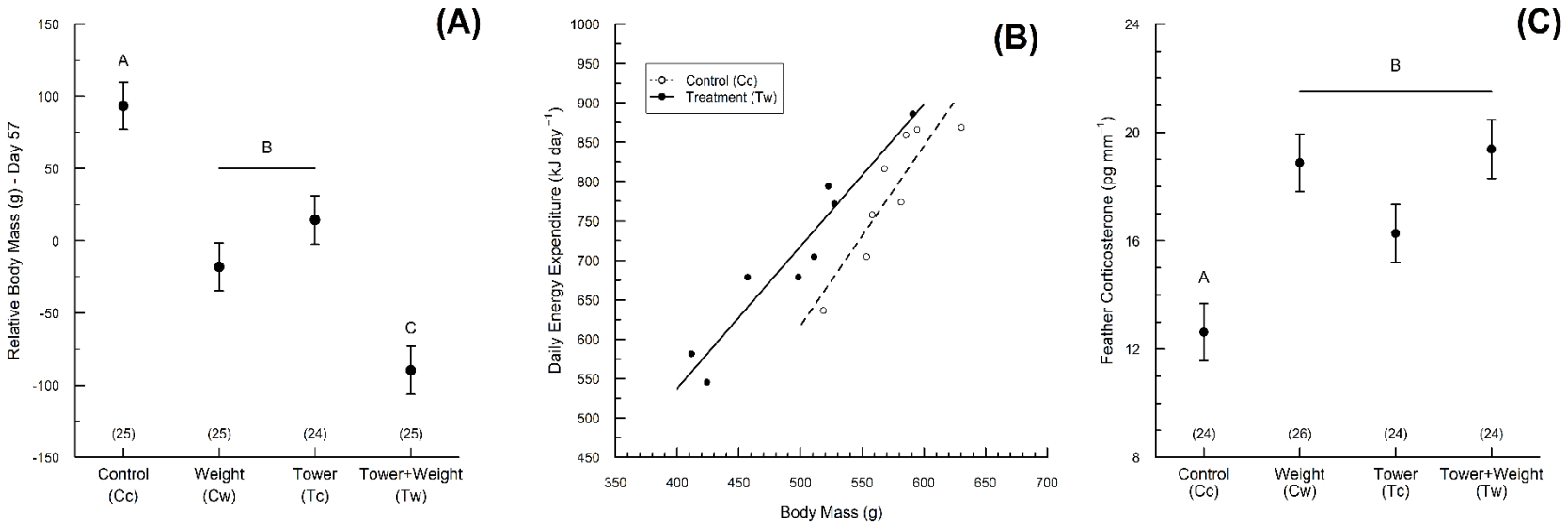

Figure 2.2. Experimental results – Phase One: Relationships between body mass, energy expenditure and feather corticosterone in relation to workload. (Panel A) Predicted relative body mass (LS mean ± SE) corrected for initial body mass of captive female mallards following 48-day exposure to workload treatments (elevated towers and obstacles and/or, carrying back-mounted loads) and relative to controls. Body mass values are corrected for differences between rooms. (Panel B) Daily energy expenditure (DEE) of 24-day old mallard ducklings at start of wing feather growth, controlled for body mass in workload treatment (Tw: closed circles) and controls (Cc: open circles). (Panel C) Feather corticosterone ($CORT_f$) measured in wing feathers (mean ± SE) in relation to workload treatment groups in 57-day old captive mallard ducklings. Capital letters denote treatments that are not significantly different from each other and bracketed numbers represent sample sizes.

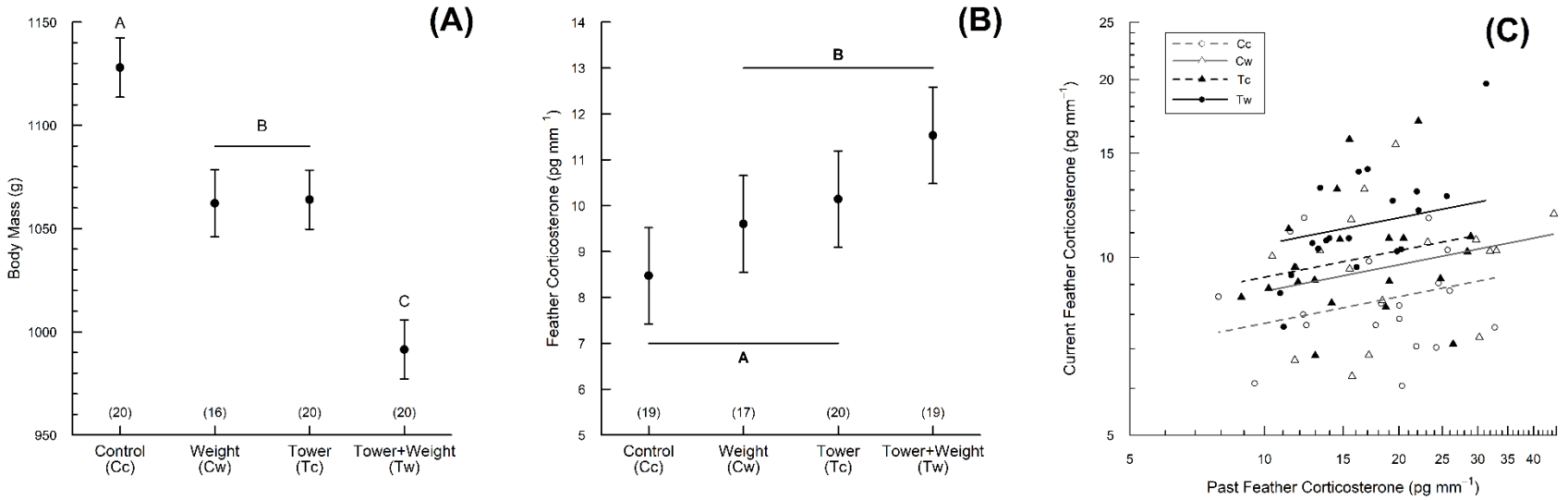

Figure 2.3. Experimental results – Phase Two: Relationships between body mass and feather corticosterone in relation to workload. (Panel A) Body mass (mean ± SE) corrected for initial body size of 133-day old captive female mallards following 38-day exposure to workload treatments (elevated towers and obstacles and/or, carrying back-mounted loads) relative to controls. (Panel B) Feather corticosterone ($CORT_f$) measured in re-grown mallard wing feathers (mean ± SE), corrected for prior $CORT_f$ values, in relation to workload treatment groups. (Panel C) Mean $CORT_f$ in relation to workload treatment groups. Capital letters denote treatments that are not significantly different from each other and bracketed numbers represent sample sizes.

CHAPTER 3. COMBINING FEATHER-BASED MEASURES OF STABLE ISOTOPES AND CORTICOSTERONE TO LINK GEOGRAPHY, PHYSIOLOGY AND REPRODUCTION ACROSS THE ANNUAL CYCLE OF A MIGRATORY BIRD: CASE STUDY OF NORTHERN PINTAILS.

3.1 Introduction

An individuals' state or condition prior to breeding is an important determinant of reproductive investment and subsequent success, particularly in waterfowl. Birds in lower body condition may arrive and initiate breeding later, invest less in reproduction, have poor reproductive success, or may even forgo breeding entirely (Ankney and MacInnes 1978, Krapu 1981, Alisauskas and Ankney 1992, Bêty et al. 2003, Blums et al. 2005, Devries et al. 2008*b*, Warren et al. 2014). As early-nesting females generally lay larger clutches (Ankney and MacInnes 1978) and produce more surviving offspring (Guyn and Clark 1999, Blums et al. 2002), delayed breeding due to low body condition (i.e., low nutrient reserves used for egg-laying and incubation) may result in lower reproductive success or survival compared to conspecifics (Blums et al. 2005, Devries et al. 2008b). Environmental conditions and events that are both spatially and temporally separated from breeding periods not only impact individual condition, but the habitats, resources and environments encountered during non-breeding periods also have important implications for future reproductive investment and performance (Ankney and MacInnes 1978, Norris 2005, Newton 2006, Norris and Marra 2007). Therefore, assessing the downstream consequences of past events on future reproduction is important for understanding the full suite of factors that influence individual reproductive success.

Termed carry-over effects (COEs), the impacts of non-lethal events and processes which occur in one season can carry forward to other seasons; requiring adjustments or altering performance in subsequent seasons (Sedinger and Alisauskas 2014). Changes in food availability, habitat, weather, or timing can influence an individual's condition or state as well as performance in the future (Harrison et al. 2011, 2013). For example, the use of suboptimal habitat during the winter period can result in lower body condition and impair subsequent reproductive performance (Marra and Holberton 1998, Gunnarsson et al. 2006, Inger et al. 2010, Legagneux et al. 2012). Yet studies identifying the impacts of COEs on individual condition, breeding performance or identifying geographic regions where such COEs originate are limited, often due to challenges in following individuals throughout the annual cycle (Inger et al. 2010).

Traditional capture or collection of individuals at specific locations can provide site- and season-specific information on condition or reproductive investment (Miller 1986, Esler and Grand 1994, Bêty et al. 2003, Devink et al. 2008) but lack the ability to track individuals through time. Although external markers overcome many of these obstacles, interpretations may be confounded by altered behaviour and performance (Cox and Afton 1998, Guyn and Clark 1999, Barron et al. 2010) or results may be hampered due to marker loss, detection failure during subsequent searches and can be cost-prohibitive. Alternatively, natural intrinsic markers which are incorporated into tissues can represent a record of both geographic and physiologic history, potentially providing valuable information for addressing questions about COEs (Hobson 1999, Rubenstein and Hobson 2004).

Animal tissues retain a record of prior environments through the incorporation of stable isotopes and this process has provided valuable insight into migratory pathways, diet composition and habitat use for a wide variety of species (Hobson and Clark 1992, Hobson 1999). As a result of biogeochemical processes that are specific to the local food web, stable isotope signatures are passed to consumers feeding within the local environment (Peterson and Fry 1987). The length of time that tissues retain location-specific isotopic signatures is determined by isotope turnover rates (Hobson and Clark 1992) and in the case of inert keratinous tissue such as feathers, isotopic signatures at the time of feather synthesis are retained until the feather is lost or replaced (Hobson 1999). A stable isotope of hydrogen, deuterium ($\delta\ ^{2}$H), varies in relation to precipitation gradients across North America (Bowen et al. 2005), where $\delta\ ^{2}$H values in feathers correlate with mean growing-season $\delta\ ^{2}$H values in precipitation, inferring geographic origins of feather growth across broad regions (Clark et al. 2006, 2009, Hobson and Wassenaar 2008, Hobson et al. 2012). A suite of stable isotopes, including carbon (^{13}C), nitrogen (^{15}N) and sulphur (^{34}S) can also be used to identify feather origins. Sulfur and carbon isotopes have been used to separate marine vs. freshwater food webs (Lott et al. 2003), while carbon isotopes provide information about photosynthetic pathways and assist in differentiating between mesic and xeric habitats, as well as in-shore and off-shore feeding habits (Hobson and Sealy 1991, Hobson 1999, Rubenstein and Hobson 2004). Nitrogen isotopes reflect feeding trophic position and may be enriched in terrestrial environments due to agricultural inputs (Kelly 2000, Hebert and Wassenaar 2001, Rubenstein and Hobson 2004). Multi-isotope approaches have been successfully used to differentiate biomes and predict geographic origins to help identify natal,

wintering and molting areas for waterfowl (Hebert and Wassenaar 2005*a*, *b*, Clark et al. 2006, 2009, Fox et al. 2007, Yerkes et al. 2008, Hobson et al. 2009, Inger et al. 2010). Recently, addition of auxiliary information from banding, migration routes and even genetics have further refined location assignments of unmarked individuals (Van Wilgenburg and Hobson 2011, Chabot et al. 2012, Guillemain et al. 2014, Hobson et al. 2015).

Feather tissues not only incorporate stable isotopes but can also provide a record of physiological state. Glucocorticoid hormones are an important physiological mediator in maintaining energy balance in response to predictable (i.e., growth, migration, reproduction) and unpredictable events and environmental changes (Sapolsky et al. 2000, McEwen and Wingfield 2003, Romero 2004, Landys et al. 2006, Wingfield and Romero 2015). In birds, measurements of corticosterone from plasma have provided an intrinsic physiological measurement of habitat quality (Marra and Holberton 1998, Müller et al. 2007), food availability, weather conditions and individual condition (Kitaysky et al. 1999, Angelier et al. 2010). Importantly, corticosterone is incorporated into growing feathers ($CORT_f$) and provides an integrated record of hormone response during the period of feather growth ranging from days to weeks (Bortolotti et al. 2008, Lattin et al. 2011, Jenni-Eiermann et al. 2015). As feathers from different plumage tracts grow during different seasons and thus geographic locations, $CORT_f$ can be used to provide insight into an individual's energetic state during multiple seasons when moult chronology is known.

Previous studies have found relationships between $CORT_f$ and body condition, reproductive parameters and the surrounding environment (review in Romero and Fairhurst 2016) and investigated potential COEs using $CORT_f$ from previous time periods, finding relationships for individual condition and future breeding performance (Crossin et al. 2013, Kouwenberg et al. 2013, Harms et al. 2015, Latta et al. 2016). However, results are not consistent across species (Legagneux et al. 2013, Bourgeon et al. 2014, Boves et al. 2016, Hansen et al. 2016), and only recently have studies examined COEs using $CORT_f$ in waterfowl outside of marine and arctic breeding species (see Chapter 2).

Northern pintail populations (*Anas acuta*) are a species of conservation concern and remain below North American conservation objectives likely due to reductions in reproductive success of birds settling in the cropland-dominated prairie region (Miller and Duncan 1999, Podruzny et al. 2002, NAWMP 2012, Clark et al. 2014). Grassland regions are more productive

for breeding pintails compared to annual cropland dominated areas, as grasslands support higher nest densities, greater nest survival rates, and higher proportion of older birds compared to agricultural areas (Kowalchuk 2014), and higher proportions of perennial cover are associated with an overall increase in waterfowl nest survival rates (Howerter et al. 2014). While most of the continental pintail population breeds in the grassland-cropland landscape matrix of the prairies, declines in regional productivity suggest that reproductive success on the prairies may be impacted (Podruzny et al. 2002, Hebert and Wassenaar 2005*a*). Pintails typically arrive to the prairies in early spring and rely more upon endogenous reserves in comparison to other prairie-breeding waterfowl species (Clark et al. 2014), creating the possibility for COEs to influence reproductive success as reported for several arctic-nesting waterfowl (Ankney and MacInnes 1978, Esler and Grand 1994, Inger et al. 2010, Harms et al. 2015). For example, eiders with higher levels of $CORT_f$ arrived to breeding grounds later and in lower body condition, which led to reductions in reproductive success and survival during an outbreak of avian cholera (Harms et al. 2015). While much is known about survival, energetics and body condition in breeding and wintering pintails (Esler and Grand 1994, Cox et al. 1998, Miller and Newton 1999, Ballard et al. 2004, Lee et al. 2007, Moon et al. 2007), less is known about other phases of the annual cycle such as during moult and migration (Dombrowski et al. 2003, Miller et al. 2005, Yerkes et al. 2008, Fox et al. 2014) or whether conditions experienced in prior seasons influence future performance.

The use of feather biomarkers provides a unique approach to investigating how past conditions during non-breeding periods could impact future performance and limited studies have linked isotopes to measures of physiology (Kouwenberg et al. 2013, Fairhurst et al. 2013b, Bourgeon et al. 2014, Harms et al. 2015, Warne et al. 2015, Fairhurst et al. 2017, Fleming et al. 2018). Combining stable isotopes and $CORT_f$ information from a single feather is a relatively new approach that informs patterns in reproductive investment (Kouwenberg et al. 2013), habitat and physiology relationships (Fairhurst et al. 2013b), health and migratory timing (Warne et al. 2015), and foraging patterns (Fairhurst et al. 2015). Isotopes can provide insight into the geographic location of moult as well as the composition of, or resources in the surrounding environment. $CORT_f$ provides energetic context during the period of feather growth (see Chapter 2) and has potential for novel tests of COE hypotheses. Utilizing feathers from different tracts, a temporal series can be used to investigate effects across an annual cycle. Therefore, I used a suite

of stable isotopes to determine moult location and insight into antecedent environmental conditions in female northern pintails, while levels of $CORT_f$ were used to index past physiological state. My objectives were to: **1)** identify pre- and post-breeding moult location for prairie-nesting pintails using stable isotopes, **2)** determine if specific landscapes, environments or regions influenced patterns in measures of energetic state ($CORT_f$), and **3)** examine if indices of reproductive success (body condition during breeding and nest initiation date) are influenced by either past geographic origins or physiologic state. I predicted that variation in $CORT_f$ would vary with the location of feather growth and that body condition and nest initiation date would be negatively related to $CORT_f$ as found in other migratory species.

3.2 Methods

3.2.1 Study Areas

Breeding northern pintails were captured and monitored in southern Saskatchewan in 2011 and 2012 (Figure 3.1). More detailed description of study sites can be found in Chapter 5 (Figure 5.1).

3.2.2 Sample Collection

Beginning the first week of May each year, crews systematically searched approximately 780 ha of potential nesting habitat at cropland- and grassland-dominated sites, three times over approximately 3-week intervals (Klett et al. 1986, Devries et al. 2008a, Skone et al. 2016). Due to low nest success, particularly for nests initiated early in the season and to increase sample size, small non-electrified predator-deflection fences (Sargeant et al. 1974) were deployed around pintail nests when found in stages of late laying (egg count ≥ 5) or incubation. Approximately 15% and 40% of all discovered pintail nests were fenced in 2011 and 2012.

Late-incubating females were captured up to 5 days prior to the estimated hatch date using mist nets, or walk-in, spring-loaded or automatic nest traps (Weller 1957, Coulter 1958, Bacon and Evrard 1990, Dietz et al. 1994). Morphometric measurements of wing (± 1.0 mm with a wing ruler), head-bill and total tarsal (± 0.1 mm with dial calipers) lengths and body mass (± 10 g with a Pesola spring scale) were recorded. I digitally photographed the extended right wing and collected the 5^{th} greater secondary covert (GSC) feather and several flank feathers. Female age was classified as either second-year (i.e., yearling = SY) or after-second year (i.e., adult = ASY),

based on wing feather characteristics (Duncan 1985) and comparison with a known age feather collection (K. Guyn 2000). I also recorded landscape type and estimated nest initiation date based on incubation stage and clutch size (Weller 1956). All capture and handling protocols were approved under University of Saskatchewan Animal Care protocol (20110039), and by provincial and federal scientific research permits (12FW118, 11-SK-SC013 and 10458D). More detailed nest search and female capture methodologies can be found in Chapter 5.

3.2.3 Feather Corticosterone

I measured levels of corticosterone in wing ($CORT_{fw}$) and body ($CORT_{fb}$) feathers following procedures established by Bortolotti et al. (2008). Briefly, feathers were measured and weighed with the calamus removed and minced into approximately < 5 mm^2 pieces. I then added 10 mL of methanol (HPLC grade, Fisher Scientific, Fair Lawn, NJ, USA) to feather samples, sonicated for 30 min at room temperature and then incubated overnight in a 50 °C water bath. The methanol extract was separated from feather material through vacuum filtration using a polyester fiber plug. Feather material, sample vial and filter were washed twice with an additional 5 mL of methanol, which was added to the original extract. Extract methanol solution was left to evaporate under a fume hood for 48 h. Extraction residues were reconstituted in 600 mL of a phosphate buffer system (PBS; 0.05M, pH 7.6) and frozen at -20 °C until radioimmunoassay was performed using a corticosterone antibody (Sigma Chemicals, St. Louis, MI, USA, product No. C8784). I assessed $CORT_f$ extraction efficiency by spiking three additional feather samples with a small amount (~ 5000 CPM) of [^{3}H] corticosterone prior to extraction and recovered > 95 % of the radioactivity within reconstituted samples. All wing and body feathers were randomized twice; during extraction and prior to radioimmunoassay, with all samples run blind and measured in duplicate. Assay variability was assessed using the coefficient of variation (CV) of known standards run in duplicate across all assays, with a limit of 15% CV (±SD) as used in previously published $CORT_f$ literature (Bortolotti et al. 2008). Average intra-assay variation was 6.9 % (range 5.4 - 9.4 %) and inter-assay variation was 13.0 %. Serial dilutions of pintail feather samples revealed displacement curves that were parallel to standard curves. As feathers are believed to grow in a time-dependent rather than mass-dependent manner, I expressed [$CORT_f$] by unit of feather length (pg mm^{-1}; Bortolotti et al. 2008, Jenni-

Eiermann 2015, Romero and Fairhurst 2016). All $CORT_f$ analysis was performed at the University of Saskatchewan, Canada.

3.2.4 Stable Isotopes

I measured stable isotopes of hydrogen ($^2H/^1H$), carbon ($^{13}C/^{12}C$), nitrogen ($^{15}N/^{14}N$) and sulfur ($^{34}S/^{32}S$) in wing and flank feather samples extracted for $CORT_f$ (see above). Feather pieces were cleaned using a 2:1 chloroform:methanol wash and air-dried for 24 h under a fume hood. The distal tip of each feather, excluding the rachis, was used for isotope analysis. Samples were analysed at the University of California-Davis Stable Isotope Facility (Davis, CA, USA). For stable hydrogen (δ^2H) isotope analysis, approximately 1.25 mg of feather material was packaged into silver capsules and analyzed using the comparative equilibration method described by Wassenaar and Hobson (2003). Stable hydrogen analysis was performed using high temperature (1345 °C) flash pyrolysis of samples using an Elementar PyroCube (Elementar Analysensysteme GmbH, Hannau, Germany) interfaced with a PDZ Europa 20-20 (Sercon Ltd., Chesire, UK) continuous-flow isotope ratio mass spectrometer (CF-IRMS). All stable isotope values are reported in standard δ notation per mil (‰) relative to international standards (Table B1). Replicates of laboratory keratin reference standards revealed repeatability errors of ±1.3 ‰ and ±1.9 ‰ for wing and body feathers, respectively.

For carbon-13 ($\delta\ ^{13}C$), nitrogen-15 ($\delta\ ^{15}N$) and sulfur-34 ($\delta\ ^{34}S$) analysis, approximately 1.25 -2.00 mg samples of feather material were packed into tin capsules. Carbon and nitrogen samples were analyzed using standard CF-IRMS techniques with a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK); sulfur isotope analysis used an Elementar vario ISOTOPE cube elemental analyzer and pre-concentration unit interfaced with a Sercon 20-22 IRMS (Sercon Ltd., Cheshire, UK). Measurement errors were ±0.2‰ for $\delta\ ^{34}S$ and ±0.3‰ for $\delta\ ^{15}N$ and $\delta\ ^{13}C$. Feather samples were interspersed with known laboratory keratin standards and calibrated against standard reference materials (Table B.1).

3.2.5 Moult Chronology

Northern pintails undergo multiple complete and partial feather moults each year (Clark et al. 2014). A pre-formative moult occurs approximately 3 weeks post-hatch, when natal down is replaced by tail, flank and scapular feathers and followed by body, head, and wing feathers by

6 weeks in age (Clark et al 2014). Beginning in the late-summer and continuing into the fall, fledged ducklings undergo a second, incomplete pre-formative moult (Pyle 2008) where larger body feathers, scapulars and upper wing coverts are developed and replaced; however, primary, tertial, and secondary wing feathers are retained (Miller 1986, Smith and Sheeley 1993). In late winter and early spring, a female's cryptic body plumage is developed in both hatch year and adult birds during a partial definitive pre-alternate body moult on the non-breeding grounds (Pyle 2008) and during the post-nesting period, adult females undergo a definitive pre-basic moult associated with synchronous wing feather replacement. Unsuccessful or non-breeding females may also undertake moult migration in anticipation of pre-basic wing moult (Pyle 2008, Clark et al. 2014). Based on these moult patterns I assumed that isotopic and hormone signatures contained within wing feathers (5^{th} GSC) of nesting females represent post-breeding (adults) or natal (yearlings) origins from the previous summer, and body feathers (flank) represent preceding late winter or spring migration origins.

3.2.6 Geographic Assignment

The geographic origins of prior feather moult were estimated using a multi-isotopic assignment approach informed by individual isotopic signatures measured in wing (e.g., informs moult location after breeding the previous summer) and body (e.g., informs previous winter-spring moult location) feathers from breeding female northern pintails. I used multiple data sets to inform classification and assignment. First, I used *(i)* a multi-isotopic ($\delta\,^{13}$C, $\delta\,^{15}$N, $\delta\,^{34}$S) classification scheme based on previous studies of North American waterfowl (Hebert and Wassenaar 2005*a*, *b*, Yerkes et al. 2008) to broadly classify origins to major biome and aquatic system. I then created *(ii)* a probabilistic surface of moult origins based on continental precipitation data and constrained by pintail distribution. I further refined the potential wintering origins using a Bayesian likelihood-based assignment framework to narrow potential origins by incorporating uncertainty and producing a probabilistic estimation of moult origin (Van Wilgenburg and Hobson, 2011, Guillemain et al. 2014).

(i) Multi-isotopic classification

I combined isotope assignment methods previously developed for North American waterfowl and, when possible, those specifically for northern pintails (Hebert and Wassenaar 2005*a*, *b*, Yerkes et al. 2008, Coulton et al. 2010). Birds feeding in coastal environments

typically have higher $\delta^{34}S$ values and lower $\delta^{13}C$ values compared to inland-feeding conspecifics (Kelly 2000, Lott et al. 2003, Rubenstein and Hobson 2004, Yerkes et al. 2008) and isotopes in feathers vary with land use in prairie Canada, as more negative values of $\delta^{34}S$ and positive values of $\delta^{15}N$ are found in waterfowl feathers collected from agricultural regions (Herbert and Wassenaar 2001, 2005*b*, Clark et al. 2006, Yerkes et al. 2008, Coulton et al. 2010). Therefore, individuals were classified as coastal origins based on cut-offs of $\delta^{34}S$ (> 10‰) and $\delta^{13}C$ (> -19 ‰) in wing or body feathers and as originating from agricultural habitats based on $\delta^{15}N$ (> 10‰) and $\delta^{34}S$ (> 2‰) values in wing feathers. Herbert and Wassenaar's (2005*b*) classification tree used $\delta^{2}H, \delta^{13}C, \delta^{15}N$, and $\delta^{34}S$ values to correctly classify 80% of pintail duckling origins based on known-location feathers, which I used to separate female moulting locations into prairies, boreal or Alaska biomes. The Pacific coast and Central Valley of California as well as the Gulf coast of Texas and Louisiana provide important wintering habitat for pintails in North America (Hestback 1993) and can be differentiated using $\delta^{15}N$ isotopes (Herbert and Wassenaar 2005a, Clark et al. 2006). I made assumptions that isotopic thresholds for claws were similar to feathers and classified pintails using $\delta^{15}N$ thresholds, with breakpoints as the Pacific Coast (PC; ≤ 10‰), Gulf Coast (GC; ≥ 11.5‰) and assigned intermediate values as Mid-Continent (MC).

(ii) Probabilistic assignment

Likely moult origins were refined using large-scale spatial variation in δ^{2}H values, where a GIS-based continental-scale model of the amount-weighted growing season precipitation hydrogen values ($\delta^{2}H_p$; Bowen et al. 2005) from the Global Network of Isotopes in Precipitation (GNIP) database (IAEA/WMO 2001). The precipitation isoscape was converted to a predicted feather isoscape ($\delta^{2}H_f$) based on previously established relationships between precipitation and feathers derived from known-origin waterfowl ($\delta^{2}H_f$ = -31.6 + 0.93 ‰ $\delta^{2}H_p$) developed by Clark et al. (2006, 2009) and constrained within the breeding and non-breeding ranges for pintails in North America (BirdLife International and NatureServe 2014). For body feathers only, I then used a Bayesian likelihood-based assignment approach to incorporate estimates of uncertainty and prior probabilities of pintails from Saskatchewan being found in each flyway based on hunter harvest data (Hobson et al. 2009, Van Wilgenburg and Hobson 2011). For each feather sample, I calculated the probability that a given cell (resolution: 0.33°

latitude by 0.33° latitude by longitude) within the δ^2H_f isoscape represented the origin of the individual based on the normal probability density function:

$$f(y^*|\mu_c, \sigma_c) = \left(\frac{1}{\sqrt{2\pi}\sigma_c}\right) exp\left[-\frac{1}{2\pi\sigma_c^2}(y^* - \mu_c)^2\right] \quad (4.1)$$

where $f(y^*|\mu_c, \sigma_c)$ is the likelihood that a given cell within the δ^2H_f isoscape (c), represents the potential origin for an individual of unknown origin (y^*), given the predicted mean δ^2H_f value for that cell (μ_c) and the estimated standard deviation of δ^2H_f values of individuals growing feathers at the location (σ_c). To factor in uncertainty, I used the standard deviation of the residuals from the precipitation-feather isotope conversion equation (σ = 11.67 ‰) from Clark et al. (2009). Each individual feather then had a separate probability density surface of likely origins, and for body feathers only, incorporated the probabilities of flyway origin (f_m) using band recovery data (see Section 2.2.5) using Baye's rule:

$$f_x = \frac{f(y^*|\mu_c, \sigma_c)f_m}{\sum_i f(y^*|\mu_c, \pi_c)f_m} \quad (4.2)$$

where the numerator represents the product of the likelihood of observing δ^2H_f at any cell of the isoscape estimated by Eq. 1 and spatially explicit prior probabilities of origin estimated from band recovery with each flyway (f_m). To estimate likely location, I used a 3:1 odds ratio to balance between potential error in classification and geographic resolution, where the upper 75% of estimated probabilities derived from Eq. 2, were coded as 1 and all others as 0, thereby creating a binary map for each individual (Van Wilgenburg and Hobson 2011). I then summed the binary maps for all individuals and rescaled the posterior probabilities (f_x) relative to maximum values using an odds ratio approach (Van Wilgenburg and Hobson 2011), creating separate probability isoscape surfaces for both wing and body feathers in each year.

The above geographic assignment was conducted using code developed by S. Van Wilgenburg (Canadian Wildlife Service, Saskatoon, unpublished) and the 'raster' package (Hijmans 2015) in the R statistical program (R Core Team 2015). As pintails may spend non-breeding periods in coastal environments (Clark et al. 2014) which may mislead geographic assignment due to relatively high δ^2H values from marine inputs (Lott et al. 2003, Yerkes et al. 2008), geographic origin was not estimated for individuals that were classified as moulting in

coastal regions (see above). Lastly, I estimated the latitude of moult for body feathers using the center of gravity derived from the probability density surfaces for each bird.

3.2.7 Band Recovery

The Prairie Pothole Region (PPR) spans multiple migratory flyways (Pacific, Central, Mississippi and Atlantic) and pintails nesting within the PPR can vary in flyway affinities, impacting the likelihood of geographic origins. To refined potential body feather moult locations I used direct recovery data for northern pintails banded in the prairies of northern United States and Canada to inform posterior probabilities during probabilistic assignment (see above). To limit analysis to the most relevant locations and time periods, I restricted banding and recovery data between years 2004 – 2014 and recovery records from banding locations between longitudes -102°W and -111°W and between latitude 48°N and 52°N (Figure 3.1). Since the proportion of birds shot in each flyway shifts based on banding location (increase in Pacific flyway recoveries at western banding locations), I binned banding data into two regions (East and West) using an approximate mid-point longitude (-106°W) between capture locations. Direct band recovery records from within Canada or Alaska were removed to ensure harvest location was representative of southward migratory movement. The proportion of birds shot in each flyway was calculated from banding totals in each region to supply prior probabilities (f_m) during geographic assignment. For example, a nesting female captured in 2011 (western banding region) would have a prior weighting of 0.56 applied to cells falling within the Pacific flyway, and a prior weighting of 0.26 and 0.18 for cells within the Central and Mississippi flyways (Table 3.1).

3.2.8 Statistical Analysis

I initially explored for the presence of confounding variables and examined whether there were annual (2011/2012), female age (ASY/SY) or landscape (Crop/Grass) level differences in feather isotope values. I then examined if female age, moult landscape type (wing = agricultural vs. non-agricultural; body = coastal vs. inland), or biome (BIO: wing = PR, BO, or AK; body = PC, MC, or GC) influenced $CORT_f$, and used analysis of variance and step-wise removal of non-significant terms to refine final variables of interest. To examine if individual stable isotopes were associated with variation in $CORT_f$, I used general linear models and information-theoretic model selection criteria (AIC_c; Akaike's Information Criterion adjusted for sample size) to test

for patterns in $CORT_f$, as explained by $\delta^{2}H, \delta^{13}C, \delta^{15}N$, and $\delta^{34}S$. Two individuals were identified as outliers in the $CORT_f$ measurements and removed from analysis. All $CORT_f$ values were mean centered by year to correct for site/year effects.

To determine if past physiologic conditions or geographic locations influenced subsequent reproductive success, I used two indices hypothesized to be important predictors of reproductive performance in waterfowl (body condition and nest initiation date). Body condition was estimated using a scaled mass index (SMI) using wing length to account for overall structural size (Peig and Green 2009) and mean-centered by year to correct for annual variation. Birds with missing body mass or wing length measurements (n = 10) were retained in the dataset but assigned an average value for the missing metric. Relative nest initiation date (NID) was calculated as nest initiation date minus the 5% nest date in each year; divided by maximum. General linear models were used to determine if body condition and relative nest initiation date were influenced by location and COEs from prior periods, including; winter biome, aquatic system, and both linear and quadratic interrelationships with $CORT_{fb}$. To control for known effects of declining body condition throughout the nesting season, I included body condition index as a variable to be considered in the nest initiation date models. I also tested for interrelationships between wintering latitude of pintails and reproductive parameters by adding the estimated winter moult latitude (LAT) to the best-approximating model to see if it improved model fit.

To reduce the risk for overparameterization of models, given sample size, I limited analysis to main effects only. I considered all combinations of main effects (excluding interactions) and ranked competing models using weighted AIC_c (Burnham et al. 2002). Within each model set, the model with the smallest AIC_c value was considered most parsimonious. Multiple models within two AIC_c units of the best-approximating model (≤ 2 ΔAIC_c values) are considered competitive (Burnham and Anderson 2002) however, I only interpreted the most parsimonious nested model (Arnold et al. 2010). Residuals from the top model were assessed for normality and the standardized parameter estimates ($\beta \pm$ SE) are presented unless otherwise stated. All analyses were conducted within R statistical software (R Core Team 2015).

3.3 Results

3.3.1 Breeding Season Effects

I captured 103 nesting female pintails, of which 80 (2011: n = 34; 2012: n = 46) provided complete isotopic, glucocorticoid, morphological and reproductive data. The number of captured birds in grassland-dominated landscapes was 26.5% in 2011 compared to 54.3% of the sample in 2012, while the proportion of first-time breeders differed between years, with 32.4% of birds in 2011 classified as SYs and 47.8% of the sample in 2012. As birds were captured during a larger study on duckling survival, a completely balanced design was not possible and differences in sample composition do not reflect pintail landscape or habitat selection. There was no evidence that body condition, nest initiation date differed between landscape type (Ps ≥ 0.09) or female age (Ps ≥ 0.16) however, all three variables did differ by site-year. Mean (± SE) body condition was higher in 2011 (638.2 ± 8.1 g) compared to 2012 (625.7 ± 6.4 g) and for captured birds, the first nest initiation date occurred 17 days earlier in 2012 (April 11th) compared to 2011 (April 28th). Differences in nest initiation dates may be due to higher early nest losses in 2011, where early nesting birds that failed were not adequately sampled.

Isotope values for each year are listed in Table 3.2 and displayed graphically by feather type (Figures. B.1 and B.2). The $\delta^{2}H$ values in wing feathers differed between years (ANOVA, $F_{(1,85)}$ = 5.91, P < 0.02) but not by landscape type (P = 0.54), female age (P = 0.38) or their interaction (P = 0.34). Similarly, $\delta^{34}S$ differed by year only ($F_{(1,85)}$ = 9.69, P < 0.01), where birds nesting in southwestern Saskatchewan in 2011 had a lower mean (± SE) $\delta^{2}H$ values (-146 ± 3.0 ‰) and higher $\delta^{34}S$ values (-4.7 ± 1.5 ‰) compared to birds captured in southeastern Saskatchewan in 2012 ($\delta^{2}H$ = -137 ± 2.1 ‰; $\delta^{34}S$ = -10.5 ± 1.2 ‰). I found no evidence that $\delta^{13}C$ in wing feathers varied by female age, breeding landscape, year or their interaction (P ≥ 0.29); however, $\delta^{15}N$ did vary with landscape type ($F_{(1,85)}$ = 8.54, P < 0.01) but not year or age (P ≥ 0.26). Birds nesting in grassland landscapes had lower mean $\delta^{15}N$ values (8.6 ± 0.3 ‰) - compared to cropland landscapes (9.8 ± 0.3 ‰).

Similarly, variation in body feather $\delta^{2}H$ values was best explained by year ($F_{(1,82}$ = 12.07, P < 0.01), but was unrelated to age or landscape type (P ≥ 0.27). Mean δ^{2}H values were lower in 2011 (-111 ± 3.2 ‰, n = 38) compared to 2012 (-97 ± 2.6 ‰, n = 46) and I found no evidence that variation in $\delta^{13}C$, $\delta^{15}N$ or $\delta^{34}S$ isotopes from body feathers differed between ages, breeding landscapes, or years (P ≥ 0.29).

3.3.2 Moult Origins: Multi-isotope Classification and Geographic Assignment

In total, 16,737 female pintails were banded in the greater study region between 2004 and 2014 (Figure 3.1), of which 338 were recovered during the subsequent hunting season with a mean annual direct recovery rate of 2.4 ± 0.4% (range: 1.5% - 3.3%). Pintails banded in the western area (n = 171 recoveries) were primarily harvested in the Pacific flyway (56%), followed by the Central (26%) and Mississippi (18%) flyways, with only a single record from the Atlantic flyway, while pintails banded in the eastern region (n = 167 recoveries) were harvested at the highest rates in the Mississippi flyway (45%), followed by the Central (42%) and Pacific (13%) flyways (see Table 3.1).

Isotopic assignment of wing feathers indicated that only a single bird showed evidence of marine origins and most remaining birds were classified as moulting in the Prairies, followed by signatures consistent with moult origins from Alaska and Boreal biomes (Table 3.3; Figure B.3) while the majority of prairie-moulting birds had isotopic signatures consistent with agricultural landscapes (52.5%, n = 32). Results from the likelihood-based assignment of individuals to the $\delta\,^{2}H_{f}$ isoscape were similar as most pintails were assigned to isotopic contours consistent with Canada's prairie and prairie parkland regions or Alaska (Figure 3.3). The range in $\delta\,^{2}$H values measured from wing feathers was from -202 to -108 ‰, covering most of continental Canadian territories and western provinces, Alaska and portions of North Dakota, Montana and Wyoming. Three quarters of the sample (n = 44) had values falling between -154 to -129.5 ‰ (Figure 3.2) which corresponds to the Prairie and Boreal Plains ecozone that extends from British Columbia to northern Manitoba and southwestern Nunavut and encompasses the Prairie, Boreal Plains, Boreal Shield and Taiga Shield Ecozones as well as central Alaska.

In comparison, relatively equal proportions of birds moulted body feathers in coastal areas or between the three general wintering areas of the Pacific coast and California, Mid-continent and the Gulf coast of Louisiana and Texas (Table 3.3; Figure B.3). Flank feathers also showed large variation $\delta\,^{2}H_{f}$; ranging between -143 to -52 ‰ and 75% of samples occurred between -117 to -90 ‰, which corresponds to a band running from southern British Columbia, through the Pacific northwestern states, Idaho, Wyoming and Colorado then extending through Nebraska, the Dakotas and into southern Manitoba. These mid-latitude origins are likely associated with spring migration and match results of spring migration studies (Pearse et al. 2011), with higher likelihoods towards the Pacific northwest and California in 2011 and mid-

continent and gulf coast in 2012 (Figure 3.2). Based on likelihood assignments the estimated moult latitudes for wing feathers ranged between 47°N and 63°N, while flank feathers ranged between 28°N and 55°N (Figure 3.2).

3.3.3 Feather Corticosterone and Carry-Over Effects on Reproduction

Pearson correlations indicate that $CORT_{fw}$ was not correlated with $CORT_{fb}$ (r = 0.13, P = 0.27) and I found no evidence that variation in $CORT_{fw}$ was explained by biome (ANOVA, $F_{2,75}$ = 0.48, P = 0.62) or landscape type (P = 0.34) but did differ between ages (P = 0.06); where adult pintails had higher levels of $CORT_{fw}$ (LS mean; 0.31 ± 0.37) compared to first-year breeders (-0.78 ± 0.44). Isotopically, variation in $CORT_{fw}$ was best explained by a model including the δ^2H isotope alone (β = -0.20 ± 0.11) however, this model explained little variation (R^2 = 0.03) and the intercept only model was highly competitive (Table 3.4); therefore, the top model was not interpreted further and the effect of δ^2H deemed negligible.

Similarly, variation in $CORT_{fb}$ was not related to predicted biome (ANOVA, $F_{1,63}$ = 0.01, P = 0.95), aquatic system (P = 0.81) or female age (P = 0.92), however there was a positive correlation between $CORT_{fb}$ and the δ^2H isotope (Pearson, r = 0.27, P = 0.03), which was highlighted in the top model explaining variation in $CORT_{fb}$ as the δ^2H isotope was the only term in the top ranked model (Table 3.5). Lower $CORT_{fb}$ levels (β = 0.27 ± 0.12) occurred more often at higher hydrogen isotope values or more northern latitudes (Figure 3.3), however this parameter was not estimated with high precision and explained little variation (R^2 = 0.06).

The intercept-only model was the top model explaining variation in body condition, as no relationships occurred with wintering biome, aquatic system, $CORT_{fb}$ values or nest initiation date (Table 3.6). The addition of predicted moult latitude did not improve model fit (Δ AICc = 1.28). Multiple competitive models best explained variation in relative nest initiation date (Table 3.7) with the most parsimonious nested model (R^2 = 0.16) containing parameters for aquatic system (β = -0.26 ± 0.22) and $CORT_{fb}$ (β = 0.35 ± 0.11). Birds that nested later in the season had higher levels of $CORT_f$ in body feathers grown on the wintering grounds or during spring migration and overall, birds from coastal landscapes had later relative nest initiation dates compared to birds of inland origin (Figure 3.4). As predicted moult latitude was partially correlated with $CORT_{fb}$ (Pearson; r = -0.26, P = 0.03) I did not include both terms in the same

model but instead substituted latitude in place of $CORT_{fb}$ within the top ranked model, yet fit was not improved (Δ AICc = 8.82, R^2 = 0.05).

3.4 Discussion

Intrinsic markers in feathers are carried with individuals throughout the annual cycle and allow for inference into both the geographic location and physiological state of the individual during periods of feather growth. Feathers grown during non-breeding periods enable consideration of potential impacts of non-lethal events from previous time periods and carry-over effects on subsequent breeding success. This study provided insight into the migratory origins of female northern pintails breeding in Saskatchewan prairies and investigated potential carry-over effects of past landscapes and environments as well as physiological state on future reproduction. Contrary to predictions, I found no evidence of strong carry-over effects from prior landscapes and environments as influencing corticosterone measured in feathers nor subsequent body condition or reproductive investment. However, I did find some support for carry-over effects of wintering environment and feather corticosterone on reproductive timing in nesting pintails, and this should be investigated further during future studies.

3.4.1 Migratory Origins

Using isotopic thresholds developed by previous studies, I did not detect differences in the isotopic composition of feathers between adults and juveniles or between cropland and grassland dominated landscapes and any differences were associated with site-year variation. These results highlight the plasticity and mobility of female pintails nesting on the Canadian prairies as both adults and juveniles, originating from multiple moult locations were found in both landscape types. Annual differences were detected in δ^{2}H values in wing and body feathers but are likely reflective of migratory propensity, where birds in southwestern compared to southeastern Saskatchewan had different flyway propensities. The isotopic origin maps (Figure 3.3) highlight that birds in 2011 originated predominately from western (wintering) areas where lower δ^{2}H values likely represented an overall more northerly feather moult compared to 2012. In a study of mallard feathers, variation in δ^{34}S levels were primarily related to northern environments due to various geologic, abiotic and biotic sources (Hebert and Wassenaar 2001, 2005*b*) and the higher values in δ^{34}S in 2011 may indicate that a higher proportion of birds moulted in prairie regions prior to capture in 2011. In both 2011 and 2012 values remained well

below the those associated with northern Canada but within the expected range for the prairies and the pacific coast.

Results from multi-isotopic classification (Table 3.3) suggested relatively equal distributions between flyways, which contrasted with results from the probabilistic assignment approach identifying stronger Pacific flyways propensity for southwest banded birds based on band recovery data. This discrepancy indicates that the multi-isotope classification approach likely had higher errors of omission for pacific flyways, incorrectly assigning Pacific Coast birds to either Mid-continent or Gulf Coast. A classification of mallard ducklings of known origin did have the lowest accuracy for birds originating in California (Herbert and Wassenaar 2005b) and the use of thresholds to determine wintering origin established using claws (Clark et al. 2006) may not be as effective for body feathers. This error may have been reduced if feathers were not grown during spring migration as the wide-ranging distribution of birds across latitudes likely added additional error to the classification. Feather samples could also have been collected from wintering pintails in each region for comparison. Annual parts surveys to inform harvest occur regularly occur in waterfowl and winter banding efforts could also supply winter grown feathers if moult origins were known.

Almost half of all birds moulted body feathers in inland and non-coastal habitats and while studies have found that coastal environments are important early winter habitats, it is the inland freshwater sites which may be more important for wintering waterfowl (Ballard et al. 2004, Pearse et al. 2011). The large proportion of birds that winter in coastal and estuary habitats along the Gulf of Mexico and Pacific coast highlight the importance of such regions. The number of birds using coastal areas is likely underrepresented as interregional movements between coastal regions and inland food sources are common in wintering pintails (Cox and Afton 2000) and with more northerly predicted latitudes of moult, if an inland shift occurs prior to feather moult, then coastal habitat use would not be detected with this methodology.

Lower $\delta\,^{15}$N values were found in grassland nesting birds which could indicate that wing feathers were molted in non-agricultural environments the previous year. If grassland dominated regions confer reproductive or survival benefits to nesting and moulting pintails, then females may select grassland habitats in future years based on past success or experience. Very little is known about habitat requirements during remigial wing moult and more research is required to

further understand this phase of the annual cycle as well as the physiological constraints that may be placed on individuals in preparation for southward migration (Fox et al. 2014). My results provide needed information on the moult origins of prairie nesting pintails and provide evidence towards the importance of retaining and securing grassland dominated breeding and moulting habitats for northern pintails. Future investigation should examine preferential selection in breeding and moulting pintails and whether grassland habitats are sequentially selected year upon year, particularly in relation to past performance or broad-scale habitat and wetland conditions.

3.4.2 Feather Corticosterone

Feather corticosterone can index energetic demand for both ducklings and grown waterfowl (see Chapter 2) and age-related effects in $CORT_f$ are hypothesized to reflect inexperience of juveniles in selecting and securing quality wintering habitat (Boves et al 2016). Female pintails exhibit age-specific differences between the timing of migration, where wintering adult females initiated inter-regional migration earlier than younger conspecifics (Cox and Afton 2000, Fleskes, Jarvis and Gilmer 2002). Despite this and counter to predictions, I found no evidence that corticosterone from body feathers was related to female age; however, $CORT_f$ in wing feathers was higher in adults compared to first-year breeders. Age related differences in wing feathers rather than body feathers may relate to moult chronology. Wing feathers are grown by adults post-breeding, while in first year birds, wing feather are developed on natal areas; body feathers however are grown following fall migration for both juveniles and adults. Higher levels of adult $CORT_f$ wing feathers may reflect in increased burden from breeding or demands to undergo full wing moult and prepared for fall migration. Studies of growing ducklings found similar patterns in $CORT_f$ and provide confidence that despite age related differences in wing feathers, the effects of $CORT_f$ may be more similar between juveniles and adults; however only body feathers were used for reproductive analyse.

I did not any find evidence that $CORT_f$ was related to moult location or landscape type. Numerous studies have correlated $CORT_f$ with environmental or climatic conditions such as wintering locations, habitat quality, trophic feeding patterns or temperature and precipitation (Legagneux et al. 2013, Bourgeon et al. 2014, Treen et al. 2015, Latta et al. 2016, Sorensen et al. 2016, Fairhurst et al. 2017). Although this study classified pintails across biomes (PR, BO, AK, or CA, MC, GC) and demonstrated diverse geographic origins of prairie nesting pintails (Haukos

et al. 2006), the inability to detect age or geospatial differences at a landscape scale using $CORT_f$ is consistent with some other studies (Fairhurst et al. 2013b, Fairhurst et al. 2015).

As moult of body feathers is not synchronous and varies among individuals, then assumptions that all birds moulted feathers at the same time or in the same location would likely inhibit detection of age and geographic effects. It is also unlikely that similar conditions were encountered across all biomes and therefore the lack of an effect. Both stable isotopes and $CORT_f$ exhibited large variation suggesting different environments and physiologic states and variation or lack of effect may instead result from the spatial scale that was considered. If events such as weather events, competition or variable food resources influence glucocorticoid secretion at more local scales then geospatial variation may not be reflected in coarse biome classification inferred from stable isotopes. Fairhurst et al. (2013) reported that $CORT_f$ in songbirds reflected environmental conditions and food availability at the local scale rather than landscape-level; however, I could not reliably include variables measured at local scales so was unable to assess these impacts. My results do not support the hypothesis that broad regional differences exist between wintering habitat that are reflected in $CORT_f$ and future assessments should consider longer time periods and include comparisons where more extreme changes in wintering habitat, climate oscillations or drought cycles occur (e.g. California drought) that can impact breeding pintail populations (Hestbeck 1995).

Variation in $CORT_f$ was also not strongly explained by stable isotopes. Studies investigating interrelationships between $CORT_f$ and stable isotopes are limited and have highlighted energetic advantages of feeding at higher trophic levels ($\delta^{15}N$; Fairhurst et al. 2015) and increases in $CORT_f$ at lower carbon values which index habitat change (Fairhurst et al. 2013b); however, results are not consistent for all species (Fairhurst et al. 2017) and although differences in wintering diet between inland and coastal areas have been shown to impact endogenous reserves in pintails (Yerkes et al. 2008), I did not find evidence that such dietary differences impact energetic demands as indexed by corticosterone. Unique to this study, I did find some support that $CORT_f$ in body feathers was related to their $\delta^{2}H$ values, indicating that the latitude of spring moult may have energetic consequences for wintering pintails. Pintails moulting in the southern latitudes appear to have higher levels of $CORT_f$ which could reflect the energetic demands of migration, as found in plasma corticosterone of long-distance migratory shorebirds (Landys-Ciannelli et al. 2002). Migration theory predicts that birds travelling further

distances should offset additional migratory costs by obtaining other benefits such as greater food reserves or reduced risk of predation or disease, and therefore experience lower energetic demands (Aharon-Rotman et al. 2016). This pattern has been demonstrated in Alaskan pintails, where females arriving with the greatest internal lipid reserves had traveled the longest distances (Yerkes et al. 2008). Females which moult feathers further north (i.e., shorter distances from breeding grounds) had lower levels of $CORT_f$ which may result in earlier nest initiation dates (see below). These individuals may have lower energetic demands and of higher quality, allowing for potential earlier migration and nesting and a positive effect on individual fitness. However, this hypothesis requires further examination as only a limited number of studies have found such effects and, in this study, the top model had relatively low explanatory power. Additional studies with greater sample sizes and linking to body condition or energetic management upon arrival would greatly benefit such investigations.

3.4.3 Carry-over Effects on Female Body Condition and Nest Initiation

Although $CORT_f$ can be used to index changes in energy expenditure and body condition (Harms et al. 2015, Boves et al. 2016, see Chapter 2), I found no evidence that body condition of breeding pintails was influenced by pre-breeding origins, corticosterone in body feathers or timing of breeding. Pre-breeding body condition in pintails may be influenced by both migration distance and staging habitat where birds using inland freshwater areas furthest from Alaskan breeding areas had the highest body condition upon arrival (Yerkes et al. 2008). These differences may result from poorer quality foods in coastal areas compared to freshwater habitats (Ballard et al. 2004) and the loss of important inland habitats have been associated with declines in pintail condition over time (Moon et al. 2007). Body condition may also be impacted by winter hydrologic conditions as pintail body condition increases during wet years and amplify regional effects compared to dry years (Miller 1986, Smith and Sheeley 1993, Moon and Haukos 2009). Other studies have found direct links between $CORT_f$ and body condition in both songbirds (Latta et al. 2016) and arctic nesting waterfowl (Harms et al. 2015); where associated, but negative relationships between $CORT_f$ and body condition had important implications for reproduction, survival or securing high quality territories.

Several assumptions may limit use of $CORT_f$ in this study to detect COEs on body condition of nesting pintails. As body condition was measured prior to hatch rather than at arrival, it may not reflect true individual condition as only successfully breeding birds were

sampled and birds arriving in poor condition and potentially with distinct levels of $CORT_f$ may not be included in the sample. Additionally, while winter environments impact the condition in which waterfowl depart during spring migration, a limitation of $CORT_f$ is physiologic effects can only be measured during the period of feather growth. Individuals can compensate or increase body condition during spring migration and compensation occurring outside of the period of feather growth is not reflected in $CORT_f$. Finally, the use of a scaled mass index may not accurately reflect the lipid reserves important for nesting pintails (Schamber et al. 2008).

I did find evidence that $CORT_f$ in body feathers and the moult environment influenced nest initiation dates, creating the possibility for COEs on the timing of breeding in nesting pintails. Nest initiation dates were positively related to $CORT_f$ as well as the aquatic system; where early breeding birds had lower levels of $CORT_f$ in body feathers compared to later breeding conspecifics and originated from inland areas rather than coastal environments. Pintails wintering in coastal environments may be limited by lower quality foods (Ballard et al. 2004) compared to inland environments which could explain relationships between $CORT_f$ and nest initiation date. For example, competing energetic demands could restrict a female's ability to acquire nutrient reserves necessary for feather moult and onset of northward migration (Romero et al. 2005) or initiate nesting and this delay could increase the risk of nest failure or decrease the likelihood of breeding altogether (Hansen et al. 2016). Early nesting positively influences both nest and duckling survival rates in many waterfowl species, and early-nesting is a key strategy for northern pintails. Therefore, levels of $CORT_f$ in body feathers and differences between wintering environments can impact nest initiation date; revealing a unique example of a physiological COE from wintering regions on subsequent reproduction in prairie nesting waterfowl. Similar results have been demonstrated in other species, where higher levels of $CORT_f$ have been associated with later arrival dates in arctic nesting eiders because of energetic management challenges during the non-breeding period (Harms et al. 2015), as well as in songbirds, where those wintering in higher quality habitat exhibited lower $CORT_f$ and arrived earlier on breeding grounds (Latta et al. 2016). However, in contrast to these studies, I did not find complementary $CORT_f$ -related COEs that linked higher body condition to earlier nest initiation date, a condition-timing relationship that has been found in mallards (*Anas platyrhynchos*; Devries et al. 2008b).

There is little indication that pintail survival rates have changed over time (Rice et al. 2010, Bartzen and Dufour 2017) indicating that population production likely varies in response to habitat conditions. Raveling and Heitmeyer (1989) highlight that during dry winters, winter habitat conditions can impact pintail populations (also see Osnas et al. 2016) and the reduction in good quality inland habitat during dry years may force wintering pintails populations into suboptimal habitats, such as coastal regions, potentially resulting in elevated energetic demand. Overall, the lack of differences reflected in $CORT_f$ accounted through geographic origin and the limited evidence for physiological COEs indicates that local conditions during breeding during 2011 and 2012 likely have greater influences on breeding performance compared to wintering locations alone. Considering that captured birds inherently underwent successful migration and attempted to breed, the sample may not fully represent birds which were burdened sufficiently to influence $CORT_f$ or compensation during spring migration could dampen the effects of $CORT_f$.

Pintails are highly mobile and typically shift breeding distributions between regions in response to local wetland conditions, and periods of long-term drought or wetland inundation in the prairies may impact pintail distribution across large areas (Clark et al. 2014). Such plasticity and flexible nature would favor individuals that can respond to local conditions or adjust breeding accordingly and may not constrain this species to be sensitive to COEs. Changes in pintail breeding populations have been linked to current breeding conditions where pintails can short stop during favorable years or flyover traditionally productive areas (e.g. prairies) during drought conditions. The ability to make breeding decisions based on the current environment, food supplies or local conditions on the breeding ground likely plays a larger role in comparison to wintering conditions in this species.

My results highlight the potential mechanism for which such COEs from wintering areas can be indexed in pintail populations and provide novel insight into the importance of wintering conditions for breeding pintails. Additional study would be valuable in considering patterns in $CORT_f$ during moult for both post- and non-breeding individuals and if reproductive decisions, survival or stopover ecology are predicted by $CORT_f$. Overall, carry-over effects are very much context dependent and the magnitude of effects may vary with geographic location, habitat quality or environmental conditions during feather growth.

Table 3.1. Probability of an adult female northern pintail banded near southeastern and southwestern Saskatchewan being harvested in each migratory flyway based on reported direct recoveries between 2004 and 2014.

Banding Region	Probability of Harvest by Flyway			
	Pacific	Central	Mississippi	Atlantic
Southwest	0.56 (95)	0.26 (44)	0.18 (31)	0.00 (1)
Southeast	0.13 (21)	0.42 (70)	0.45 (76)	0.00 (0)

Numbers in parentheses are direct recoveries (harvested same year as banded) and reported shot by hunters between years 2004 to 2014.

Totals of 7,769 and 8,968 females were banded in southwest and southeast regions, respectively.

Table 3.2. Mean (± SE) stable-isotope values (‰) of hydrogen ($\delta^{2}H$), carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$) and sulphur ($\delta^{34}S$) in wing and body feathers from female northern pintails sampled from southern Saskatchewan, 2011 – 2012. Number of females (n).

Feather	Year (*n*)	$\delta^{2}H$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{34}S$
Wing	2011 (38)	-146 (± 3.1)	-26.0 (± 0.5)	9.3 (± 0.3)	-4.6 (± 1.5)
	2012 (46)	-137 (± 2.2)	-26.4 (± 0.3)	9.3 (± 0.3)	-10.2 (± 1.2)
Body	2011 (38)	-111 (± 3.2)	-19.6 (± 0.6)	11.0 (± 3.2)	-2.2 (± 1.1)
	2012 (46)	-97 (± 2.6)	-18.9 (± 0.8)	10.8 (± 2.4)	-3.8 (± 0.8)

Table 3.3. Proportion of feathers classified based on feather origins to landscape type, biome and aquatic system using multiple isotopic values of wing and body feathers for female northern pintails sampled from cropland and grassland dominated landscapes at two breeding locations in southern Saskatchewan, 2011 – 2012. Sample size is indicated in brackets.

Feather	Year	Agriculture	Coastal	Alaska	Boreal	Prairies
Wing	2011	44% (17)	n/a	18% (7)	15% (6)	67% (26)
	2012	46% (23)	2% (1)	10% (5)	4% (2)	85% (41)
				Pacific Coast	Mid-Continent	Gulf Coast
Body	2011	84% (32)	42% (16)	29% (11)	34% (14)	37% (14)
	2012	85% (39)	54% (25)	39% (18)	24% (11)	37% (17)

Table 3.4. Model selection results for feather corticosterone (pg mm^{-1}) related to stable isotopes of hydrogen ($\delta^{2}H$), carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$) and sulphur ($\delta^{34}S$) measured in wing feathers from breeding female northern pintails in southern Saskatchewan, 2011 – 2012.

Model structure[1]	K[2]	LogLik[3]	AIC_c[4]	ΔAIC_c[5]	ω_i[6]
$\delta^{2}H$	3	-184.56	375.45	0.00	0.20
$\delta^{2}H + \delta^{34}S$	4	-183.90	376.34	0.90	0.13
Intercept-only	2	-186.21	376.58	1.14	0.11
$\delta^{2}H + \delta^{13}C$	4	-184.29	377.13	1.68	0.08
$\delta^{2}H + \delta^{15}N$	4	-184.36	377.26	1.81	0.08
$\delta^{34}S$	3	-185.54	377.41	1.96	0.07
$\delta^{2}H + \delta^{13}C + \delta^{34}S$	5	-183.66	378.13	2.69	0.05
$\delta^{13}C$	3	-185.91	378.14	2.70	0.05
$\delta^{15}N$	3	-185.92	378.16	2.71	0.05
$\delta^{2}H + \delta^{15}N + \delta^{34}S$	5	-183.79	378.41	2.96	0.04
$\delta^{2}H + \delta^{13}C + \delta^{15}N$	5	-184.13	379.07	3.63	0.03
$\delta^{13}C + \delta^{34}S$	4	-185.27	379.08	3.63	0.03
$\delta^{15}N + \delta^{34}S$	4	-185.37	379.28	3.83	0.03
$\delta^{13}C + \delta^{15}N$	4	-185.66	379.87	4.42	0.02
$\delta^{13}C + \delta^{15}N + \delta^{34}S$	5	-185.13	381.07	5.63	0.01
$\delta^{2}H + \delta^{13}C + \delta^{15}N + \delta^{34}S$	7	-183.06	381.69	6.24	0.01

[1] General linear models with fixed effects were used in all models.
[2] Number of parameters included in the model.
[3] Log Likelihood.
[4] Akaike Information Criterion corrected for small sample size (AIC_c).
[5] Difference in AIC_c values between each model and the model with the lowest AIC_c.
[6] The Akaike weight (ω_i) or likelihood of a model, given the set of models.

Table 3.5. Model selection results for feather corticosterone (pg mm^{-1}) related to stable isotopes of hydrogen ($\delta^{2}H$), carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$) and sulphur ($\delta^{34}S$) measured in body feathers from breeding female northern pintails in southern Saskatchewan, 2011 – 2012.

Model structure[1]	K[2]	LogLik[3]	AIC_c[4]	ΔAIC_c[5]	ω_i[6]
$\delta^{2}H$	3	-203.35	413.08	0.00	0.27
$\delta^{2}H + \delta^{34}S$	4	-202.75	414.13	1.05	0.16
$\delta^{2}H + \delta^{15}N$	4	-203.19	415.01	1.93	0.10
$\delta^{2}H + \delta^{13}C$	4	-203.34	415.32	2.24	0.09
$\delta^{2}H + \delta^{15}N + \delta^{34}S$	5	-202.38	415.73	2.65	0.07
Intercept-only	2	-205.95	416.08	3.00	0.06
$\delta^{2}H + \delta^{13}C + \delta^{34}S$	5	-202.69	416.35	3.27	0.05
$\delta^{34}S$	3	-205.20	416.77	3.69	0.04
$\delta^{2}H + \delta^{13}C + \delta^{15}N$	5	-203.18	417.33	4.26	0.03
$\delta^{13}C$	3	-205.55	417.48	4.41	0.03
$\delta^{13}C + \delta^{34}S$	4	-204.61	417.86	4.78	0.02
$\delta^{2}H + \delta^{13}C + \delta^{15}N + \delta^{34}S$	6	-202.38	418.14	5.06	0.02
$\delta^{15}N$	3	-205.94	418.26	5.18	0.02
$\delta^{15}N + \delta^{34}S$	4	-205.13	418.89	5.81	0.01
$\delta^{13}C + \delta^{15}N$	4	-205.54	419.71	6.64	0.01
$\delta^{13}C + \delta^{15}N + \delta^{34}S$	5	-204.61	420.18	7.10	0.01

[1] General linear models with fixed effects were used in all models.
[2] Number of parameters included in the model.
[3] Log Likelihood.
[4] Akaike Information Criterion corrected for small sample size (AIC_c).
[5] Difference AIC_c values between each model and the model with the lowest AIC_c.
[6] The Akaike weight (ω_i) or likelihood of a model, given the set of models.

Table 3.6. Model selection results for body condition (SMI) in relation to nest initiation date (NID), winter biome (WTR), aquatic system (AQU), and corticosterone in body feathers ($CORT_{fb}$) of female northern pintails in southern Saskatchewan, 2011 – 2012.

Model structure[1]	K[2]	LogLik[3]	AIC_c[4]	ΔAIC_c[5]	ω_i[6]
Intercept-only	2	-354.56	713.30	0.00	0.18
NID	3	-354.08	714.54	1.25	0.10
$CORT_{fb}$	3	-354.12	714.62	1.32	0.09
WTR	4	-353.00	714.63	1.34	0.09
AQU	3	-354.16	714.70	1.41	0.09
NID + WTR	5	-352.33	715.63	2.34	0.06
WTR + $CORT_{fb}$	5	-352.48	715.93	2.63	0.05
$CORT_{fb}$ + AQU	4	-353.70	716.03	2.73	0.05
NID + AQU	4	-353.86	716.36	3.06	0.04
NID + $CORT_{fb}$	4	-353.88	716.39	3.10	0.04
WTR + AQU	5	-352.74	716.45	3.16	0.04
$CORT_{fb}$ + $CORT_{fb}^2$	4	-354.12	716.87	3.58	0.03
NID + WTR + $CORT_{fb}$	6	-352.11	717.60	4.30	0.02
WTR + $CORT_{fb}$ + AQU	6	-352.19	717.77	4.47	0.02
NID + WTR + AQU	6	-352.24	717.86	4.56	0.02
NID + $CORT_{fb}$ + AQU	5	-353.59	718.15	4.85	0.02
WTR + $CORT_{fb}$ + $CORT_{fb}^2$	6	-352.48	718.33	5.03	0.01
$CORT_{fb}$ + $CORT_{fb}^2$ + AQU	5	-353.69	718.35	5.06	0.01
NID + $CORT_{fb}$ + $CORT_{fb}^2$	5	-353.74	718.44	5.14	0.01
NID + WTR + $CORT_{fb}$ + AQU	7	-351.97	719.81	6.51	0.01
NID + WTR + $CORT_{fb}$ + $CORT_{fb}^2$	7	-352.10	720.06	6.77	0.01
WTR + $CORT_{fb}$ + $CORT_{fb}^2$ + AQU	7	-352.19	720.26	6.96	0.01
NID + $CORT_{fb}$ + $CORT_{fb}^2$ + AQU	6	-353.59	720.56	7.26	0.00
GLOBAL	8	-351.97	722.38	9.08	0.00

[1] General linear models with fixed effects were used in all models.
[2] Number of parameters included in the model.
[3] Log Likelihood.
[4] Akaike Information Criterion corrected for small sample size (AIC_c).
[5] Difference AIC_c values between each model and the model with the lowest AIC_c.
[6] The Akaike weight (ω_i) or likelihood of a model, given the set of models.

Table 3.7. Model selection results for relative nest initiation dates in relation to body condition (SMI), winter biome (WTR), aquatic system (AQU) and corticosterone in body feathers ($CORT_{fb}$) of female northern pintails in southern Saskatchewan, 2011 – 2012.

Model structure[1]	K[2]	LogLik[3]	AIC_c[4]	Δ AIC_c[5]	ω_i[6]
AQU + $CORT_{fb}$	4	70.31	-131.99	0.00	0.34
AQU + $CORT_{fb}$ + $CORT_{fb}^2$	5	70.97	-130.97	1.02	0.20
AQU + $CORT_{fb}$ + SMI	5	70.42	-129.87	2.12	0.12
AQU + $CORT_{fb}$ + $CORT_{fb}^2$ + SMI	6	71.07	-128.77	3.23	0.07
$CORT_{fb}$	3	67.57	-128.77	3.23	0.07
WTR + AQU + $CORT_{fb}$	6	70.77	-128.17	3.82	0.05
$CORT_{fb}$ + $CORT_{fb}^2$	4	67.87	-127.10	4.90	0.03
WTR + AQU + $CORT_{fb}$ + $CORT_{fb}^2$	7	71.46	-127.04	4.95	0.03
$CORT_{fb}$ + SMI	4	67.81	-126.99	5.00	0.03
WTR + AQU + $CORT_{fb}$ + SMI	7	71.00	-126.13	5.86	0.02
$CORT_{fb}$ + $CORT_{fb}^2$ + SMI	5	68.11	-125.25	6.74	0.01
GLOBAL	8	71.68	-124.92	7.07	0.01
WTR + $CORT_{fb}$	5	67.78	-124.60	7.40	0.01
AQU	3	65.45	-124.53	7.47	0.01
WTR + $CORT_{fb}$ + SMI	6	68.15	-122.93	9.07	0.00
AQU + SMI	4	65.75	-122.87	9.12	0.00
WTR + $CORT_{fb}$ + $CORT_{fb}^2$	6	68.08	-122.79	9.20	0.00
Intercept-only	2	63.25	-122.32	9.67	0.00
SMI	3	63.73	-121.08	10.92	0.00
WTR + $CORT_{fb}$ + $CORT_{fb}^2$ + SMI	7	68.46	-121.06	10.94	0.00
WTR + AQU	5	65.93	-120.89	11.11	0.00
WTR + AQU + SMI	6	66.43	-119.48	12.51	0.00
WTR	4	63.51	-118.38	13.62	0.00
WTR + SMI	5	64.17	-117.37	14.62	0.00

[1] General linear models with fixed effects were used in all models.
[2] Number of parameters included in the model.
[3] Log Likelihood.
[4] Akaike Information Criterion corrected for small sample size (AIC_c).
[5] Difference AIC_c values between each model and the model with the lowest AIC_c.
[6] The Akaike weight (ω_i) or likelihood of a model, given the set of models.

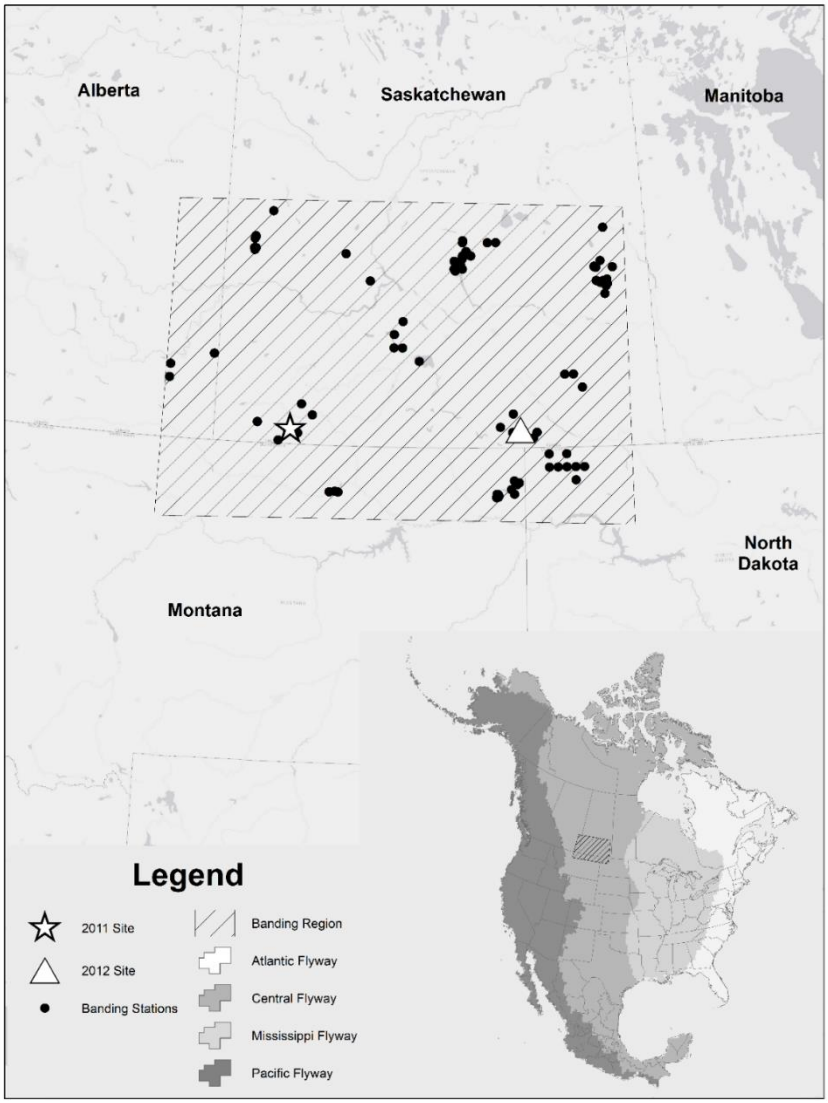

Figure 3.1. Banding locations (black dots) of northern pintails between 2004 and 2014 in proximity to study sites in 2011 (star) and 2012 (triangle) and North American migratory waterfowl flyways (Pacific, Central, Mississippi, and Atlantic; Inset Map). Detailed site layout can be found in Figure 5.1.

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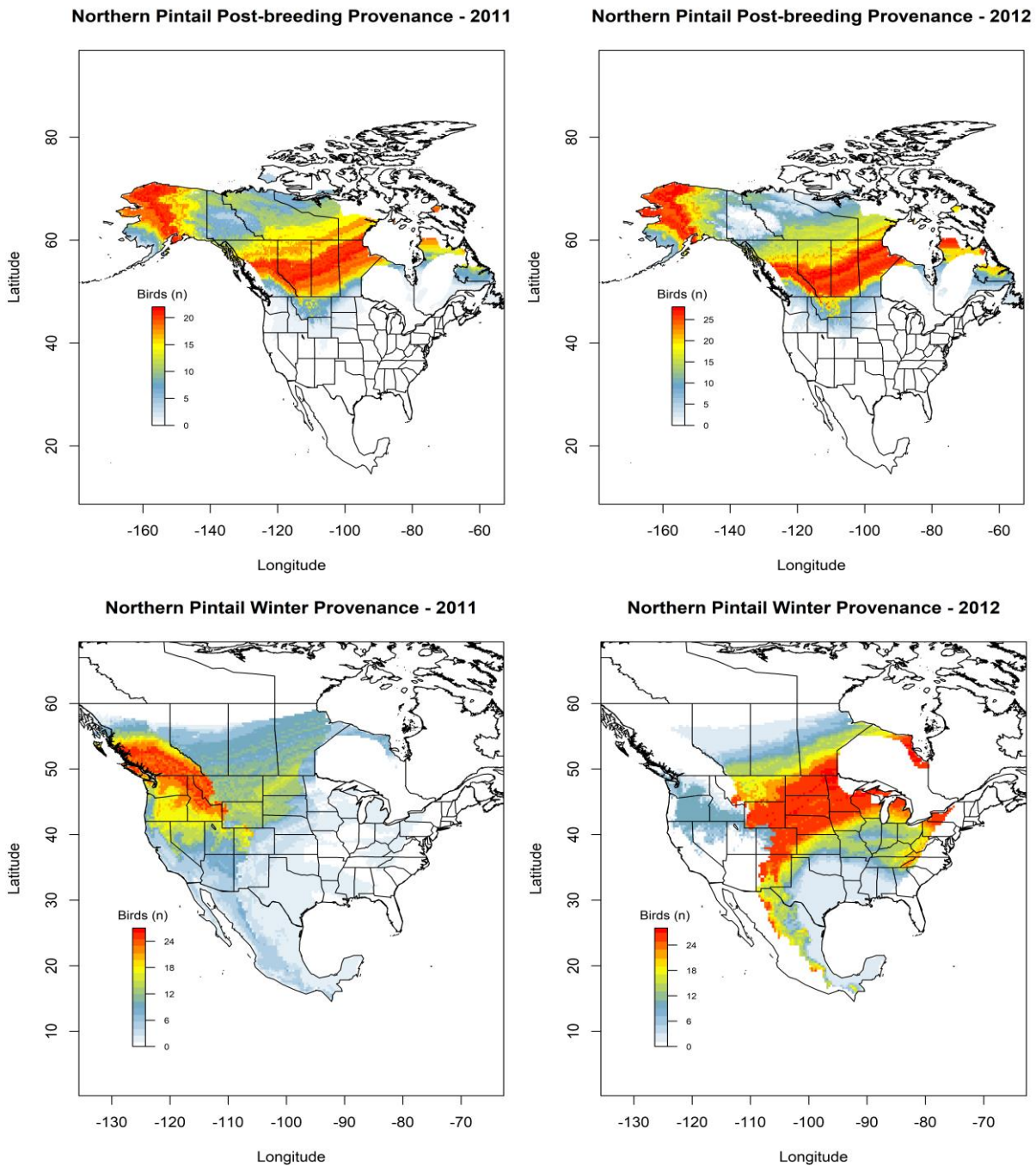

Figure 3.2. Predicted geographic distribution of moult origins for female northern pintails (*Anas acuta*) captured in Saskatchewan in 2011 (left panels) and 2012 (right panels) based on analysis of deuterium ($\delta\ ^{2}H$) values in wing (top) and body (lower) feathers. Probabilistic assignment for body feathers incorporates band recovery data for Pacific, Central and Mississippi flyways between 2004-2014 as prior probabilities. Vertical color scale bars indicate the number of birds from the total sample that are assigned to an estimated geographic location.

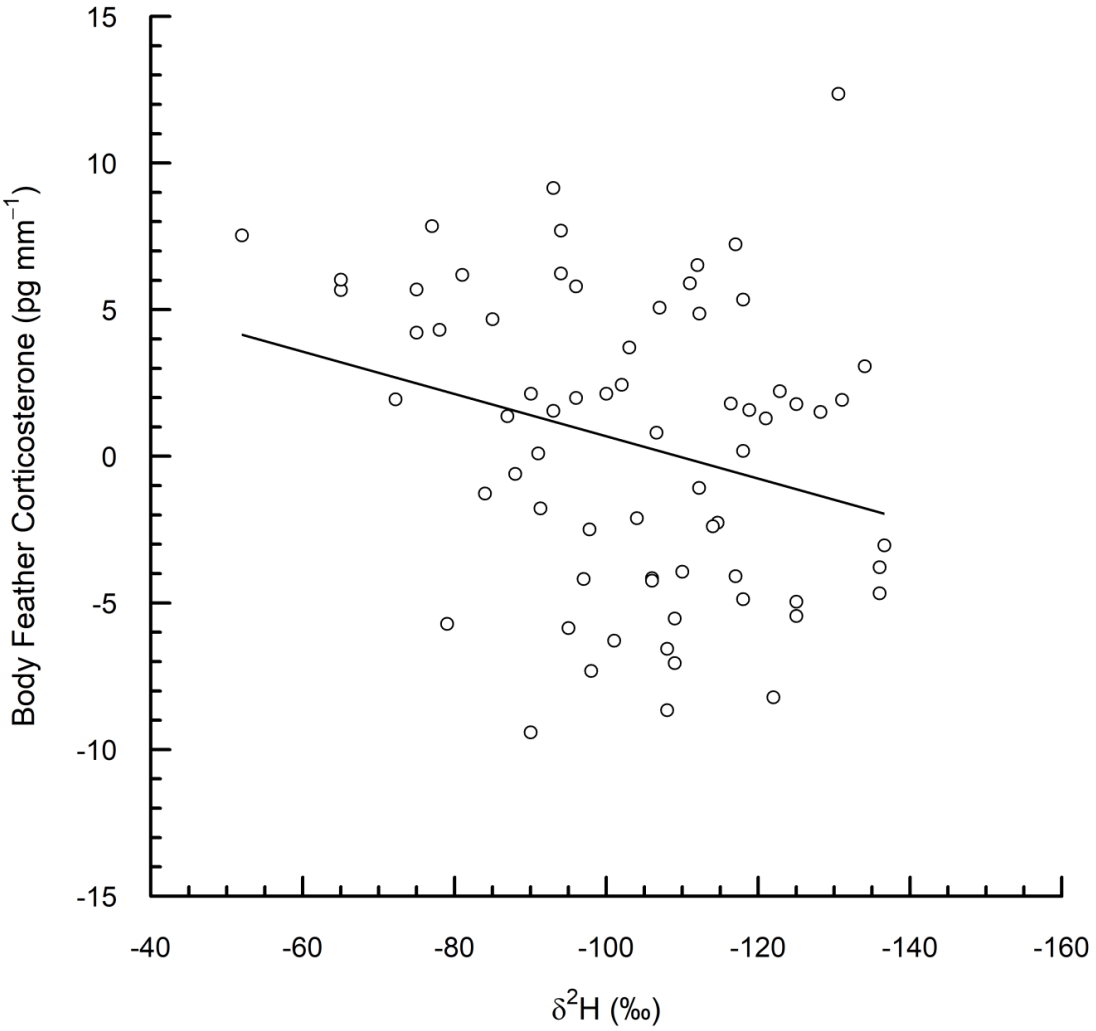

Figure 3.3. Mean-centered levels of feather corticosterone (pg mm^{-1}) relative to stable hydrogen (δ ^{2}H) isotope levels (‰) measured in body feathers of female northern pintails nesting in southern Saskatchewan, 2011 – 2012.

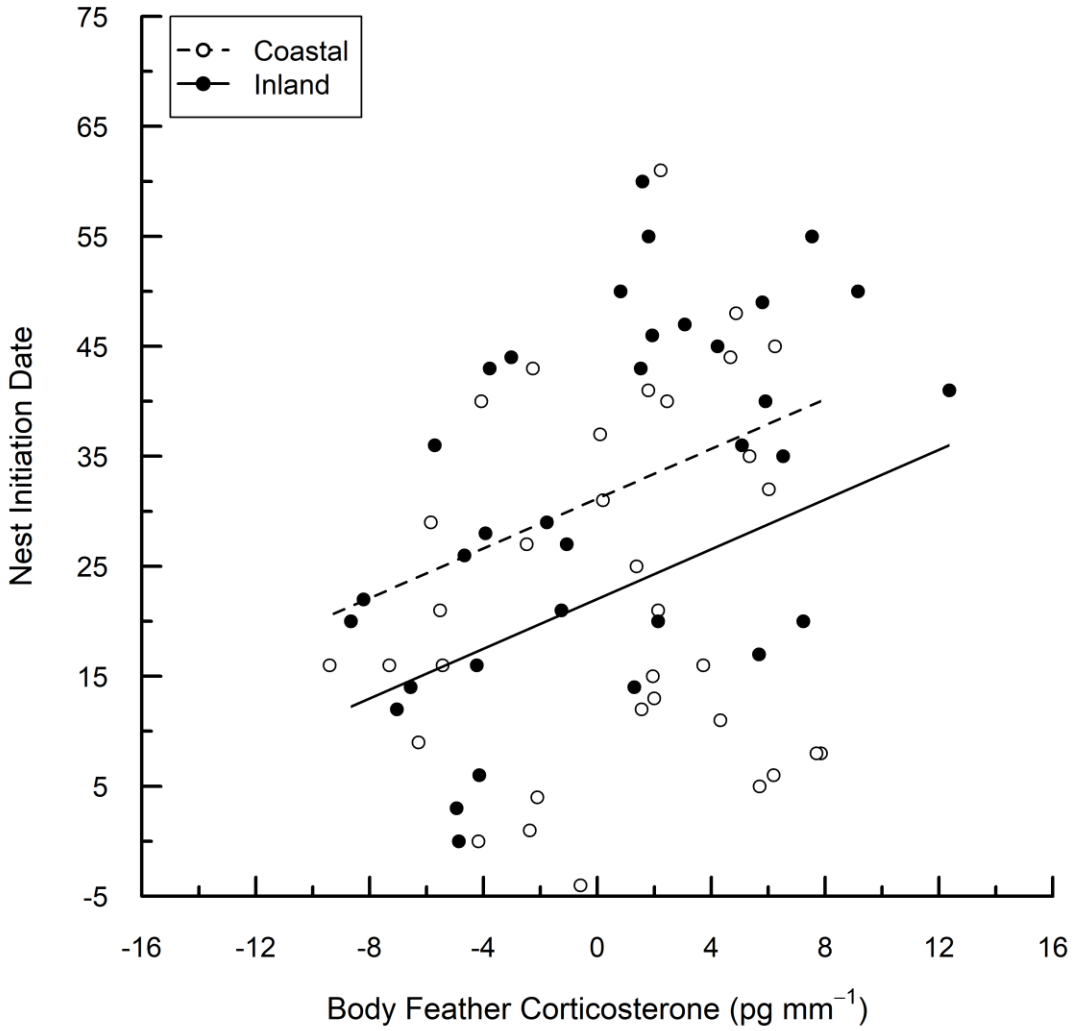

Figure 3.4. Relative nest initiation date (corrected for annual differences) as a function of feather corticosterone (pg mm^{-1}) and predicted aquatic system (open circle = coastal; closed circle = inland) derived from body feathers of female northern pintails breeding in southern Saskatchewan, 2011 – 2012

CHAPTER 4. MATERNAL INFLUENCES ON NORTHERN PINTAIL DUCKLING SURVIVAL IN SASKATCHEWAN

4.1 Introduction

The provision of parental care enables animals to enhance offspring survival and contributions to lifetime reproductive success. The amount and quality of parental investment is of general interest to ecologists as investment in current breeding is hypothesized to come at a cost to future opportunities (Lack 1966, Trivers 1972, Clutton-Brock 1991), laying a foundation for life history theory (Stearns 1989). Reproductive strategies that utilize parental care are expected when offspring survival without care would otherwise be low and the amount of care may be adjusted based on predicted environmental conditions and risks of mortality to both offspring and adults (Carlisle 1982, Clutton-Brock 1991). Most birds exhibit bi-parental care, where both sexes invest in brood success and for altricial species, investments largely consist of the provisioning of food or brood defense and vigilance for species with precocial and nidifugous young (Lazarus and Inglis 1986, Williams et al. 1994). In contrast, maternal only care occurs in less than 8% of bird species and is relatively common for waterfowl, particularly Anatidae family (Lack 1968, Cockburn 2006). Under maternal care only systems the trade-offs between current and future reproduction are not shared and variation in parental investment largely falls to the traits of an individual. Under natural selection pressures individual variation can ultimately influence population level response (Wellington 1957) and provides a unique opportunity to examine how individual heterogeneity in terms of maternal attributes contributes to offspring survival.

Effects of maternal attributes on offspring survival may manifest through inter-individual differences in timing of breeding, body condition, age or behavioural responses during brood care. Early hatching enables ducklings to take advantage of abundant resources in seasonal prairie wetlands coinciding with periods of rapid duckling growth, while females in greater body condition may be better able to devote more time towards brood rearing or securing higher quality habitats and resources. Early hatching duck broods often have higher survival, recruitment or fledging rates (Dzus and Clark 1998, Guyn and Clark 1999, Lepage et al. 1999, Arnold et al. 2004, Blums and Clark 2004; but see Gendron and Clark 2002, Amundson and Arnold 2011, Bloom et al. 2012). Brood-tending females make large investments (e.g., time,

energy, internal reserves), either actively or passively to increase the likelihood of offspring survival. Females devote approximately 6 weeks post-hatch to tending broods which come at a cost to self-maintenance and results in a life history trade-off (Trivers 1972, Carlisle 1982, Stearns 1989) with potential for reductions in future survival or reproductive success (Milonoff et al. 2004, Devries et al. 2008b, Guillemain et al. 2008). Female mallards with higher body condition have higher nest survival and earlier hatch dates (Devries et al. 2008b). Heavier females also experience greater brood success and produce more ducklings in some diving and sea ducks (Yerkes 2000, Mehl and Alisauskas 2007, Paasivaara and Pöysä 2007, Öst et al. 2008). Yet, such effects are not always consistent (Guyn and Clark 1999, Gendron and Clark 2002, Pietz et al. 2003, Howerter et al 2014). Females seek out and defend high quality brood-rearing habitats necessary for duckling growth, provide protection from inclement weather, and maintain vigilance and protection from predators. Older females may utilize past experiences to secure higher quality habitat and/or reduce risks of mortality through vigilance, aggressive or risk-averse behaviour.

While the allocation of parental care is theorized to be driven by prevailing and anticipated conditions (Carlisle 1982), inter-individual differences in the degree of care could also influence offspring survival (Dingemanse et al. 2004, Grüebler and Naef-Daenzer 2010). Behavioural syndromes are correlated behavioural responses, consistent across a variety of situations and increasingly shown to influence reproductive success and fitness (Sih et al. 2004, Groothuis and Carere 2005, Boos 2007). Behavioural profiles are often labeled as differences between fast and slow explorers, bold and cautious, or bold and shy and largely tested as an equivalent to individual personality in humans (Verbeek et al 1996). Understanding maternal influences on behavioural development is essential given their consequences for subsequent survival as individual characteristics like exploration, aggressiveness or emotionality are related to adult survival and adaptation to environmental variations (Dingemanse et al., 2004, Cockrem, 2007). For example, reactive individuals, defined as passive, motionless and shy during stressful events adapt better to unstable situations, whereas proactive individuals, defined as active, aggressive and bold do better in stable situations (Koolhaas et al., 1999; Cockrem, 2007). Associations between maternal aggression or boldness and offspring survival have been demonstrated in squirrels (Boon et al. 2007), lizards (Sinn et al. 2008) as well as birds (Dingemanse et al. 2004, Öst et al. 2008, Betini and Norris 2012, Thys et al. 2017). In red

squirrels, female aggressiveness had a positive relationship to offspring survival and its effect depended on year and food availability (Boon et al. 2007). In tree swallows, aggressive males fledged more offspring while female personality did not impact fitness (Betini and Norris 2012) and bolder female seabirds which fed further from nesting colonies had higher fitness (Patrick and Weimerskirch 2014). In nesting ducks, female mallards showed differences in risk-taking based on investment and habitat conditions (Gunness et al. 2001, Dassow et al. 2012) as well as regulatory mechanisms, habitat selection, foraging and risk-taking behaviour (Öst and Beck 2003, Ackerman et al. 2006, Kurvers et al. 2009, 2012, Seltmann et al. 2014).

Although anecdotal evidence suggests behavioural differences between females occur (Ball 1974), few examine relationships between maternal behaviour and offspring survival in waterfowl. Studies on the effects of maternal care and behaviour on offspring survival in arctic nesting geese and eiders has highlighted the importance of vigilant and aggressive behaviour (Lazarus and Inglis 1978, Williams et al. 1994, Lepage et al. 1999, Öst et al. 2008), while for prairie nesting ducks, the equivalent studies have not been done or focus on effects of hatch date and female condition (Dzus and Clark 1998, Guyn and Clark 1999, Yerkes 2000, Gendron and Clark 2002, Hoekman et al. 2004) and largely ignore behavioural traits. In this Chapter, I examine how duckling survival in a prairie-nesting duck, the northern pintail is related to maternal traits such as female age, body condition, timing of breeding and behaviour during brood-rearing.

4.2 Study Areas and Methods

4.2.1 Study Sites and Nest Searching

Detailed information on study areas, sites and capture methodology are outlined in Chapter 5. Briefly, data were collected in 2011 and 2012 at two different study areas within the Prairie Pothole Region of southern Saskatchewan, Canada. Study areas contained a mixture of landscape types, including high intensity annual crop production and contiguous tracts of native and tame grasslands. Each study areas contained multiple study sites and each site (approx. 41 km^2) was examined for one breeding season. Sites in 2011 were in southwestern Saskatchewan, within 48 km of Frontier, SK (49° 12’ N, 108° 33’W) and consisted of two grassland-dominated and four cropland-dominated sites. In 2012, sites were in west-central Saskatchewan, within 50

km of Beaubier, SK (49° 08’ N, 104° 04’ W) and consisted of two grassland-dominated and three cropland-dominated sites.

I searched for nesting female pintails using established protocols from previous studies of nesting waterfowl in the Canadian prairies (Devries et al. 2008a, Howerter et al. 2014). I conducted three complete nest searches between late April through mid-July. Searches were conducted between 06:00 – 14:00, searching all upland habitat (excluding trees, farmyards and flooded wetland vegetation) using chain or rope drags pulled with all-terrain vehicles or by hand (Klett et al. 1986, Devries et al. 2008a). For each nest, I recorded the date, time, location (UTM), habitat type, clutch size and incubation stage (Weller 1956). Nests were marked with a small piece of flagging tape, placed 10 m directly north of the nest location for added reference during female capture. Small non-electrified predator-deflection fences (Sargeant et al. 1974) were deployed around pintail nests found in late stages of laying (egg count ≥ 5) or during incubation. Approximately 15% and 40% of all pintail nests were fenced in 2011 and 2012, respectively.

4.2.2 Female Capture and Monitoring

Nests were randomly selected across a range of hatch dates and habitat types, from which I captured late-incubating females within 4 days of the estimated hatch date using walk-in, spring-loaded or automatic nest traps or mist nets (Weller 1957, Coulter 1958, Bacon and Evrad 1990, Dietz et al. 1994). I collected morphometric measurements (head, keel, and tarsus lengths, ± 1 mm with digital calipers; wing chord, ± 1 mm with a wing board ruler; and body mass, ± 10 g with a Pesola spring scale) from each captured female, digitally photograph the outstretched right wing, and collected the 5th secondary covert feather. Female age was estimated as second-year (i.e., yearling or SY) or after-second year (i.e. adult or ASY) based on plumage characteristics (Duncan 1985) and reference to a collection of known-age feathers (K. Guyn unpublished data). Females were banded with an aluminum leg band and marked with a back-mounted radio transmitter (Mauser and Jarvis 1991). To aid identification, a subset of birds (2011: n = 5, 2012: n = 52) received temporary nasal markers (modified from Lokemoen and Sharp 1985). All capture and handling protocols were approved under University of Saskatchewan Animal Care Committee standards (no. 20110039), and scientific research permits (nos. 12FW118, 11-SK-SC013, and 10458D).

Females were monitored daily using a vehicle-mounted null array telemetry antenna or handheld system (Kenward 2000). Immediately prior to the estimated hatch date the predator deflection fence was raised (approx. 15 cm) off the ground to allow females to lead newly hatched ducklings from the nest unimpeded. Broods were tracked every 1 to 7 days between hatch and 30 days post-hatch or until total brood loss, female mortality or radio-failure was confirmed. I attempted to count ducklings immediately after hatch, then weekly thereafter until tracking ceased. Counts were made using passive observation from a distance with spotting scopes or binoculars to reduce disturbance and count error. During each observation attempt, I verified female identity (i.e., nasal marker, radio antenna visible, appropriate age of young, etc.) and recorded the number and age of ducklings and if the count was considered full (i.e., all ducklings visible), partial (observer uncertain if all ducklings had been observed) or mixed (brood consisted of ducklings of different ages or species). When ducklings reached 30 days old, I performed active counts (i.e., brood drives) to confirm final brood size. I assumed total duckling loss if females abandoned broods prior to ducklings reaching 30 days in age as hen-brood bonds typically deteriorate after 40 days in age (Ringleman et al. 1982) and I made multiple observation attempts to confirm brood size or loss if females were suspected of losing a brood or a partial count was obtained (e.g., females using ponds with dense vegetation).

4.2.3 Behavioural Scores

Female behaviours were recorded using multiple indices obtained during handling or observation with each ranked on a scale of 1 – 5 (see Table 4.1). Agitation was characterized as the relative amount of physical struggling during handling (1 = calm and no struggling; 3 = some struggling; 5 = constant struggling). Aggression was scored based on the amount of scratching and biting behaviour during handling (1 = no aggressive behaviour; 2 = occasional pecking or biting; 3 = some scratching or biting; 4 = frequent scratching or biting; 5 = constant biting and scratching throughout handling). Cautiousness of brood-rearing females was recorded during brood observations and used to derive an index representing vigilance and reaction to disturbance (1 = sleeping/relaxing away from the brood (> 20 m); 2 = sleeping/relaxing in close proximity (< 20 m) to the brood; 3 = normal, watchful but relaxed; 4 = alert and may move brood into vegetation cover; 5 = alarmed and flushed from pond or led ducklings away to new pond). Overall, females that were calm in hand or stayed in the open during observations were given low rankings on respective behavioural response scales, while females that physically

struggled, scratched and bit, or immediately left the pond or hid during observations were given high rankings.

4.2.4 Model Covariates Related to Hypotheses of Interest

Model covariates were selected based on maternal factors shown or hypothesized to influence survival. Female age and body condition can influence hatch date, as older and/or females in higher body condition breed earlier than younger and lower condition females (Krapu and Doty 1979, Devries et al. 2008b, Arnold et al. 2010, Warren et al. 2013). I used feather characteristics to assign female age (**HAGE**) and selected two condition indices: scaled mass index corrected for head-bill length (**SMI**) and body mass at capture (**MASS**). I predicted that older or larger females would have higher duckling survival rates. Relative hatch date (**HATD**) was calculated based on the first predicted hatch date from all pintail nests in each year (28 May 2011, 25 May 2012). As pintails nest earlier relative to other congeners (Raquel et al. 2017), I predicted that duckling survival would be negatively associated with hatch date.

Precocial ducklings rely on maternal care early in life for habitat selection (e.g., food resources, lower competition) and protection from adverse weather (e.g., thermoregulation) and predators (avoidance, alarm cues, active defence). Personality or behavioural differences between females can alter the degree of maternal care where pintail hens that are more bold or aggressive may secure higher quality resources and locations for foraging or loafing, while hens that are vigilant, secretive, or have lower thresholds for disturbance may reduce risk of predation for offspring. To characterize cautiousness of females across the brood rearing period, I used the mean caution score derived from observations (CAUT). Because female-brood bonds weaken as ducklings grow (Ball 1975, Ringleman et al. 1982), I restricted observational scores to the period when broods were ≤ 30 days post-hatch and broods were known to be present. Aggression (AGGR) and agitation (AGIT) scores from handling were correlated with each other (Pearson r = |0.48|) so I created an additive composite variable (BEHV). All behavioural scores were not correlated with CAUT (Pearson r < |0.05|) and compared with each other to explain variation in duckling survival. I used the best-supported variable (AGGR) for subsequent modeling. Several females (n = 10) did not have caution scores obtained prior to brood loss (loss occurred prior to observation) and were assigned the sample mean score (3.38). I used a multiple linear regression to examine patterns in female cautiousness scores against behavioural scores (AGGR and AGIT), hatch date and female age. I then compared survival estimates with and without

substituted broods but found no difference in the best approximating models, so I present results from the full dataset.

4.2.5 Analysis and Survival Models

I estimated cumulative duckling survival over a period of 30 days (ϕ^{30}) using the nest survival module in Program MARK (Rotella et al. 2004, Dinsmore and Dinsmore 2007) as implemented in the RMark statistical package within Program R (Laake 2013, R Core Team 2015). The nest survival module allows estimation of survival using ragged telemetry, where exact dates of mortality are unknown. I used generalized linear models with a logit link and binomial error distribution to estimate daily survival rate (DSR) as a function of fixed covariates (Rotella et al. 2004). To partially account for site-year and duckling age effects, I included landscape type (**LAND**) and a linear duckling age term (**AGE**) as a biological baseline from which to evaluate maternal covariates. I did not allow correlated model terms (Pearson's $r >$ |0.40|) within the same model and included an intercept-only model (i.e., statistical null) for comparison.

As fates of ducklings are likely non-independent samples (e.g., brood-mates have similar fates), I followed Amundson and Arnold (2011) and estimated over-dispersion ($\hat{c} = 2.99$) using 5,000 bootstrap simulations of the biological baseline model with study site. Models were ranked using Akaike's Information Criterion adjusted for over-dispersion and sample size ($QAIC_c$; Burnham et al. 2002) and considered competitive if within ≤ 2 $\Delta QAIC_c$ units of the top ranked model. I present estimates of ϕ^{30} derived from model averaging of competitive models and display effects of individual covariates and 95% confidence intervals when other model terms are held at their mean.

4.3 Results

In total, 342 northern pintail nests were found during nest searching with 104 attending females captured across a range of hatch dates. Of radiomarked birds, only four re-nests were detected. Censoring failed nests ($n = 16$) and females/broods that died prior to leaving the nest ($n = 2$), resulted in survival histories for 262 ducklings from 41 broods in 2011 and 346 ducklings from 47 broods in 2012, and a total effective sample size of 7,964 exposure intervals. Descriptive statistics for modeled covariates are provided in Table 4.2. Cautious scores during brood-rearing were collected from 61.2% of observations ($n = 115$; 95 days) in 2011 and from 64.2% of

observations (n = 178; 84 days) in 2012, and the average length of observations was 62 min (range 0 – 240 min). I recorded the time to observation in 2012, where average latency to sighting of the female was 37.1 (± 2.5 min), and brood was 43.0 (± 2.7 min). I found no support ($F_{4,84}$ = 1.61, P = 0.179) that female cautiousness was related to behavioural scores of aggression (β = -0.05; 95% CI: -0.30, 0.19), agitation (β = -0.00; 95% CI: -0.24, 0.24), female age (β = -0.37; 95% CI: -0.06, 0.79) or hatch date (β = -0.19; 95% CI: -0.03, 0.41).

A total of 17 models were examined for maternal effects, of which three were considered highly competitive (Table 4.3). Accounting for effects of duckling age (β_{AGE} = 0.14, 95% CI: 0.118, 0.162) and landscape type ($\beta_{LAND\text{-}grass}$ = 0.55, 95% CI: 0.297, 0.806), daily duckling survival was negatively correlated with female mass (β_{MASS} = − 0.199, 95% CI: -0.315, -0.084; Figure 4.1A) and positively correlated with both hatch date (β_{HATD} = 0.240, 95% CI: 0.117, 0.364; Figure 4.1B), and cautiousness during brood-rearing (β_{CAUT} = 0.224, 95% CI: 0.064, 0.383; Figure 4.1C). Predicted cumulative survival more than doubled for cautious females (CAUT = 4, ϕ^{30} = 0.43, 95% CI: 0.36, 0.50) as compared to more relaxed females (CAUT= 2, ϕ^{30} = 0.19, 95% CI: 0.12, 0.28). Models containing hatch date and cautiousness terms alone received some support with model weights of 9.7% and 6.7% respectively; however, models containing maternal covariates of agitation or female age were not well supported (Table 4.3).

4.4 Discussion

In this study, pintail duckling survival was influenced by maternal attributes of female condition, hatch date, and a measure of cautiousness during brood-rearing. Body condition is an important determinant of waterfowl reproductive timing and effort as it can represent stored energy resources available for brood rearing. Females in poorer condition may be more likely to abandon broods earlier (Eadie et al. 1988, Bustnes and Erikstad 1991) once physiologic setpoints are surpassed (Boos et al. 2007) where brood abandonment and reductions in duckling and brood survival occur (Talent et al. 1983). In this study, I found that females which were lighter during periods immediately prior to brood hatch had higher duckling survival compared to heavier females, a result counter to my predictions. Parental care theory suggests that females should invest in offspring when further investment does not threaten its own survival (Trivers 1972) and females in lower body condition may be able to continue to invest in duckling survival if their own survival is not threatened. If sufficient wetland conditions were available throughout the

season, females in lower body condition may be able to cope with increased demands of brood-rearing without the need to abandon offspring. Reduced body condition may also be confounded with greater investment into earlier stages where smaller females, independent of age, may allocate greater proportions of resources to brood-rearing. Smaller body sizes may also benefit predator avoidance as during remex feather moult as brood-rearing females are susceptible to predation during this flightless period. Smaller body masses can aid in predator avoidance and indirectly reduce predation risk to a brood (Lima 1986, Brown and Saunders 1998, Fox et al. 2013).

The ability to capitalize on favorable habitat conditions and initiate breeding early is typically contingent on arriving with or achieving sufficient body condition upon arrival (Ankney et al. 1991, Bêty et al. 2003). Prior studies have found that females with higher pre-breeding body condition also have earlier hatch dates compared to younger or poor condition females (Devries et al. 2008b), while late-incubation body mass is positively related to nest success (Gloutney and Clark 1991) and duckling survival (Yerkes 2000, Öst et al. 2008). Additionally, measures of body mass may not reflect true body condition and while condition indices attempt to correct for differences in body mass due to structural size (Peig and Green 2009), unverified measures of mass may not accurately reflect endogenous reserves (Schamber, Esler and Flint 2009, Labocha and Hayes 2012). Overcall caution should be exercised interpreting my results as the benefits to of female mass on duckling survival are not yet known, may be confounded with unmeasured factors or may be statistically but not biologically relevant without directly testing assumptions or verifying reserves in a field setting.

Female pintails that hatched broods later in the season had higher duckling survival probabilities in this study, a result largely inconsistent with other studies of duckling survival (Rotella and Ratti 1992b, Grand and Flint 1996, Dzus and Clark 1998, Guyn and Clark 1999). Higher survival is often associated with early hatching in order to align optimized habitat conditions since wetlands in the prairies typically decline over time in quantity and quality, particularly for temporary and seasonal wetlands which are important for brood rearing. In mallards, Rotella and Ratti (1992b) and Dzus and Clark (1999) both found that duckling survival was highest in early periods when wetland densities were the greatest; while pintails in southern Alberta showed a seasonal decline in duckling survival as water levels were drawn down in a managed wetland complex (Guyn and Clark 1999). Alternatively, reduction in habitat conditions

may also lead to increased mortality risk to ducklings from avian or mammalian predators (Talent et al. 1983, Grand and Flint 1996, Pietz et al. 2003, Pearse and Ratti 2004) or a lack of adequate food (Cox et al. 1998).

If early hatching is typically associated with higher survival, then why did the opposite pattern appear in my study? Seasonal abundances of foods may appear later in the breeding season (Dawson and Clark 1996) and during the period of study, wetland conditions in southern Saskatchewan were between 32% to 55% above long-term averages (Zimpfer et al. 2012) which may represent a sustained availability of high quality habitats throughout the season. Lastly, inclement weather can also play a large role in influencing duckling survival (Pietz et al. 2003, Amundson and Arnold 2011, Bloom et al. 2012) where cold and weather is associated with mortality in ducklings. While the frequency or distribution of inclement weather was not measured directly, greater number of events that lead to mortality may be confounded with hatch date and explain why duckling survival was suppressed early in the year.

Like Guyn and Clark (1999), I found no differences in duckling survival associated with female age. Age related differences in other pintail vital rates have been documented, where adults have higher annual survival rates (Nicolai et al. 2005) and nesting densities (Kowalchuk 2014) compared to juveniles and impact timing of breeding in mallards (Krapu and Doty 1979, Devries et al 2008b). Results from this study and others suggest that such that maternal age does not play a major role in offspring survival in this species. Alternatively, measurement error in the assignment of age based on feather characteristics may have masked detecting this relationship.

This study is among the first to examine how individual brood-rearing behaviour influences duckling survival in prairie nesting waterfowl. I found that brood-rearing pintails which were more cautious, vigilant and likely to retreat to heavy cover, or leave wetlands when disturbed had higher overall duckling survival rates. Increased vigilance and antipredator behaviour can have positive effects on female fitness as maternal care for pre-fledging offspring reduces predation risk and increases offspring survival (Grüebler and Naef-Daenzer 2010). However, I did not find a non-linear relationship in brood-rearing cautiousness which suggests that I was unable to detect survival consequences of highly cautious behaviours. Pressures from natural selection would select against traits that are maladaptive, yet a spectrum of behavioural traits were observed, suggesting that there may be other conditions or scenarios where cautious

behaviour may not be beneficial. Such overly cautious behaviour may come at a cost to the attending female or brood as pintails with the highest caution scores could be observed to move broods into new wetlands. In studies of nesting mallards, risk taking behaviour was shown to vary with the relative value of offspring, with reductions in parental care when offspring survival is low (Ackerman and Eadie 2003) or if habitat conditions favor female survival (Gunnes et al. 2001). Additionally, highly reactionary responses could reduce the time females and duckling spend foraging and reduce a female's ability to energetically prepare subsequent life stages (Watson et al. 2007). Female pintails spend approximately 35% of their time on parental care activities with the rest allocated towards self-maintenance (Guinn and Batt 1985). The survival benefits of such time-consuming behaviour suggest that the benefits of parental care may benefit fitness in a manner that outweighs the costs to individuals. Anecdotally, it was also noted that pintails with broods acted at a lower disturbance threshold compared to other species (D. Johns pers. obs.). Whether this difference represented past capture experience, an individual response (as assumed in this study) or a difference between species (Ackerman et al. 2006) remains untested.

Cautiousness was not explained by agitation, aggression, hatch date or female age which suggests that this measure indexed a different behavioural response than those measured during capture and handling. A study of antipredator behaviour in birds found that while vigilance was highly repeatable across contexts, it did not correlate with aggression or boldness (Couchoux and Cresswell 2012). I also found no support that aggressive or agitative behaviour during handling was important for duckling survival. Both the agitation and aggression scores were highly correlated and may be considered a part of a behavioural syndrome. Aggressive behaviour is shown to lead to greater exploratory activities (Verbeek et al. 1996, Thys et al. 2017) which can benefit fitness (Cain and Ketterson 2012). While aggressive tendencies in arctic nesting eiders influenced brood positioning in social brood-rearing and indirectly reduced the risk of predation (Öst et al. 2006), slow-exploring tendencies in great tits were associated with greater fledging rates (Both et al. 2005). In female tree swallows, behavioural traits had no influence on reproductive success (Betini and Norris 2012). The contextual dependence of many behavioural traits may explain why I did not find an effect of aggression on duckling survival.

It should be highlighted that these results should be interpreted with caution and considered as examining exploratory hypotheses rather than testing for direct effects. Social

dynamics in paired birds or amongst a group of birds could also likely play a role as the benefits of a larger community providing vigilance will result in less time being devoted to predator vigilance (Lazarus and Inglis 1978). Pseudo replication resulting from use of individual survival metrics for non-independent brood mates and confounding site-year effects may limit inference. In addition, brood observations were collected using ordinal data, repeated across individuals. Studies of vigilance behaviour in pink-footed geese, found that subtle behavioural changes were the most influential (Lazarus and Inglis 1978) and these types of behaviours may not be detected by a composite ranking score.

Ranked scores from non-standardized observations may not provide true indices of behavioural response or traits and future studies should collect quantitative measures of behaviour to enable assessment of behavioural syndromes and correct for pseudo replication between multiple observations. The use of standardized handling or disturbance protocols is highly suggested to evaluate behavioural consistency outside of a controlled environment such as standardized disturbance tests prior to observation. It also cannot be assured that observation effects did not alter the behavioural response of attending females (i.e., Hawthorne effect), where the presence of observer bias influences the measured trait (e.g., caution score) rather than being representative across the large population. Passive observation at longer distances and during set periods of the day or brood-rearing period could reduce risk of bias. The large range in length of the observation and latency to counts highlight the variation in observation situations as a result of topography, the amount of cover on the wetland or for hiding the observer. Observations from a greater distance may not elicit the same reactions as observations obtained near the brood. While consistency of cautiousness across individuals is yet undetermined, this study does provide novel information towards how maternal care plays a role in influencing offspring survival to a greater extent than other previously tested maternal conditions.

Table 4.1. Scoring chart for measurement of female behaviour in northern pintail females.

Score	Handling Agitation	Aggression	Observation Cautiousness
1	No fidgeting / Quiet	Timid / Calm	Sleeping/relaxing away from the brood
2			Sleeping/relaxing near brood
3	Some struggling	Some scratching / Biting	Normal, watchful but relaxed
4			Alert for most of the observation and sought cover with brood
5	Constant struggling	Constant biting / Scratching	Alarmed and left pond with brood

Table 4.2. Covariates of interest explaining variation in northern pintail duckling survival in southern Saskatchewan, 2011 – 2012.

Variable	Definition	Predicted Response	Mean ± SD (min. – max.) *
CROP	Landscape Type	-	(Crop vs. Grass)
AGE	Duckling age – days	+	(1 – 30 days)
HAGE	Hen age (SY, ASY)	+	N (ASY = 49; SY = 39)
HATD	Hatch date (relative)	−	35.7 ± 18.9 (1 – 76)
MASS	Hen body mass – g (capture)	+	632.3 ± 42.6 (540 – 760)
AGIT	Hen agitation score (handling)	+	2.7 ± 1.4 (1 – 5)
AGGR	Hen aggression score (handling)	+	1.9 ± 1.2 (1 – 5)
CAUT	Hen cautiousness score (obs.)	±	3.4 ± 0.7 (1 – 5)

Covariate predicted responses are displayed as positive (+), negative (-) or neutral (±) effects. *Mean ± SD (min. – max.) are displayed for each maternal covariate.

Table 4.3. Model selection results examining maternal factors influencing pintail duckling survival in southern Saskatchewan, 2011 – 2012. Displayed are the statistical null, biological null and all candidate models better supported than the biological null. Shown for each model are the number of estimable parameters (*k*), Quasi-likelihood Akaike's Information Criterion adjusted for sample size ($QAIC_c$), change in criteria from top model ($\Delta QAIC_c$), model weight (*w*) and -2 Log-Likelihood (*-2LogLik*).

Model Terms	*k*	*QAICc*	*Δ QAICc*	*w*	*-2LogLik*
AGE + LAND + HATD + CAUT	5	605.19	0.00	0.29	1779.59
AGE + LAND + MASS + CAUT	5	605.64	0.45	0.23	1780.94
AGE + LAND + MASS + HATD	5	607.08	1.89	0.11	1785.24
AGE + LAND + HATD	4	607.31	2.12	0.10	1791.92
AGE + LAND + CAUT	4	608.02	2.83	0.07	1794.05
AGE + LAND + HATD + AGGR	5	608.84	3.65	0.05	1790.49
AGE + LAND + HAGE + HATD	5	608.85	3.66	0.05	1790.54
AGE + CAUT	3	609.41	4.22	0.04	1804.19
AGE (Biological Null)	2	614.51	9.32	0.00	1825.41
NULL (Statistical Null)	1	736.70	131.51	0.00	2196.74

* Number of estimable parameters
† Akaike's Information Criterion adjusted for sample size and overdispersion
‡ Difference in $QAIC_c$ compared to the best-approximating model
⁑ Model weight
** -2 x Log-Likelihood

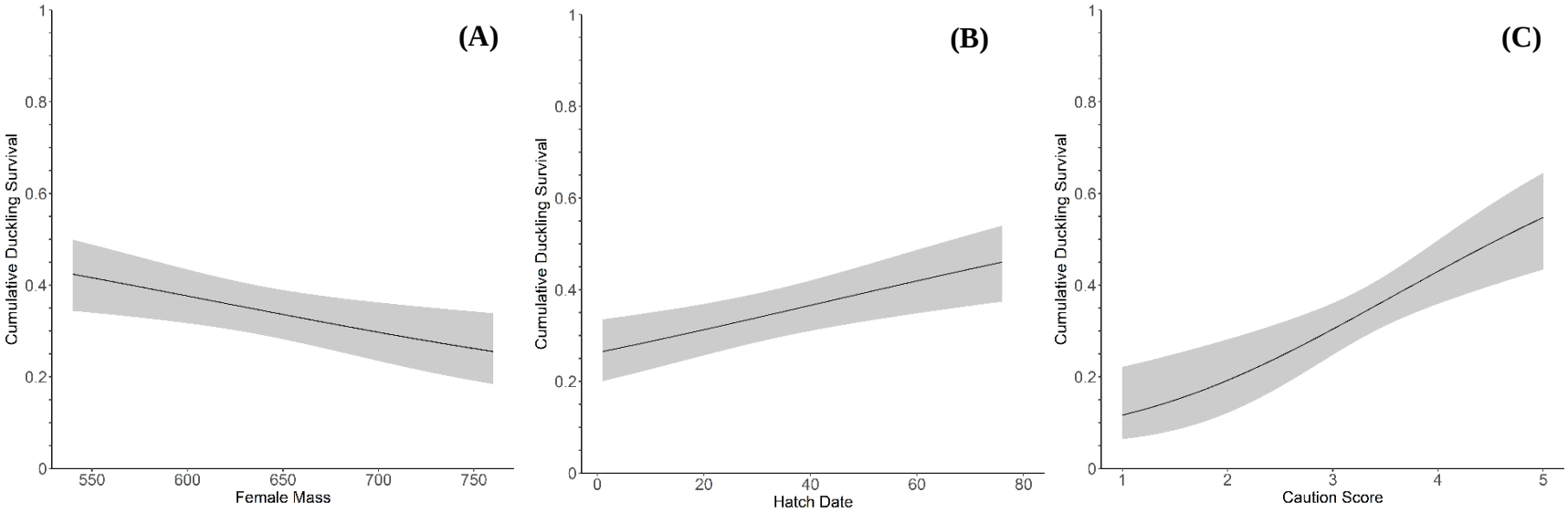

Figure 4.1. Model averaged estimates of important maternal effect influencing cumulative 30–day survival (ϕ^{30}) with 95% confidence intervals (light grey) of northern pintail duckling survival rates in southern Saskatchewan, in 2011 and 2012. Estimated survival was based on model averaged survival which included duckling age, landscape type, and combinations of (A) female mass, (B) hatch date and (C) cautiousness.

CHAPTER 5. SURVIVAL TRADE-OFFS FOR NORTHERN PINTAIL (*ANAS ACUTA*) DUCKLINGS IN RELATION TO AGRICULTURAL LANDSCAPE COMPOSITION

5.1 Introduction

The Prairie Pothole Region (PPR) is one of the North America's most important waterfowl breeding regions, where high densities of glacial depression wetlands (i.e., potholes) and remnant mixed grass prairie provide important staging, nesting and brood rearing habitat for migrating and breeding waterfowl (Doherty et al. 2018). Yet, continued agricultural intensification within the PPR may threaten long-term capacity to meet waterfowl population objectives. Shifts in cropping practices such as the reduction of idle cropland, cultivation of native grassland and drainage of wetlands across the PPR may reduce the quality and abundance of waterfowl breeding habitat (Bethke and Nudds 1995, Watmough et al. 2017) and contribute to declines some populations such as northern pintail.

The PPR has experienced excellent wetland conditions over the past decade and unlike other waterfowl species, northern pintail populations have yet to respond positively and remain below management objectives (Miller and Duncan 1999, Podruzny et al. 2002, Austin et al. 2014, Zimpfer et al. 2015). Key hypotheses for a lack of population recovery includes low reproductive success due to agricultural intensification and conservation tillage (Devries et al. 2008a, Zhao et. al 2019) and higher nest predation rates in modified upland habitats (Miller and Duncan 1999, Podruzny et al. 2002, Miller et al. 2003). In addition, pintails often nest earlier and in cropland at higher rates relative to other waterfowl species (Klett et al. 1988, Greenwood et al. 1995, Raquel et al. 2016, Devries et al. 2018) and nests established early in the breeding season can be lost to annual seeding operations (Devries and Duncan 2018). Widespread and established use of continuous cropping and conservation tillage across the PPR results in less idle land and refugia from agricultural nest destruction (Best 1986). These effects may only further exacerbate nest losses and supress reproductive success (Higgins 1977, Cowan 1982, Miller and Duncan 1999, Podruzny et al. 2002, Devries et al. 2008a, Duncan and Devries 2018).

Despite higher nest survival rates in grassland relative to spring-seeded cropland habitats (Greenwood et al. 1995, Richkus 2002) large-scale grassland restoration in the PPR is cost-prohibitive given persistent demands for cultivated land and high commodity prices (PHJV

2016). Fall-seeded cereal crops such as winter wheat have been promoted as a method to increase waterfowl nest success in cropland-dominated landscapes (Duebbert and Kantrud 1987, Cowardin et al. 1985, Miller et al. 2003, Devries et al. 2008a, Prairie Habitat Joint Venture 2016, Skone et al. 2016). Unlike spring-seeded crops, fall-seeded crops are relatively undisturbed early in the nesting season, provide nest concealment and support higher nest survival rates (Duebbert and Kantrud 1987, Devries et al. 2008a, Skone et al. 2016). However, the benefits of higher nesting success in fall-seeded crops may be lost if duckling survival in cropland-dominated landscapes is low.

Studies that have estimated pintail duckling survival in the prairies are limited but suggest that survival is lower in cropland-dominated landscapes (17% - 41%; Peterson 1999) as compared to grasslands (42% - 65%; Guyn and Clark 1999). No studies have yet concurrently measured duckling survival in intensively cropped versus grassland landscapes. Thus, direct comparison of pintail duckling survival rates between grassland- and cropland-dominated landscapes and habitats is required to adequately assess potential differences in pintail productivity.

Conservation actions like targeted deployment of fall-seeded croplands or restoration of grasslands may also be optimized by considering landscape level effects and potential trade-offs with pintail reproductive success. Landscape composition has profound implications for a variety of waterfowl vital rates. For example, pintail nest survival was positively related to the amount of perennial cover in a landscape (Devries et al. 2018) as it was for mallard (*Anas platyrhynchos*) females and nests (Greenwood et al. 1995, Howerter et al. 2014) or displayed non-linear effects (Stephens et al. 2005). Yet, larger areas of perennial cover support diverse predator communities (Phillips et al. 2001) and may drive negative relationships between duckling survival and amount of perennial cover (Krapu et al. 2000, Amundson and Arnold 2011, Bloom et al. 2012). Agricultural intensification within the PPR has reduced the abundance of smaller temporary wetlands through drainage, filling or diversion to larger permanent basins. Differences in the amount and composition of wetlands between cropland-dominated and grassland-dominated landscapes also may influence duckling survival rates as seasonal and semi-permanent wetland area have positive correlations with and duckling survival (Dzus and Clark 1998, Pietz et al. 2003, Amundson and Arnold 2011, Bloom et al. 2012, Howerter et al. 2014).

Landscape configuration also may play an important role as foraging patterns of common prairie nest predators focus along edge habitats (Larivière and Messier 2000, Phillips 2001, Phillips et al. 2003, 2004), and further nest-wetland distances necessitate longer overland movements to reach water which equate to higher risks of predation for broods and attendant females (Duncan 1987, Rotella and Ratti 1992a). The proximity and fragmentation of grassland and wetlands is also shown to effect nest survival (Howerter et al. 2014, Devries et al. 2018) and duckling mortality (Rotella and Ratti 1992a, Bloom et al. 2012). Lastly, relative timing of breeding can affect duckling survival as sparse upland and wetland vegetation and seasonal water drawdown may increase brood exposure early and late in the year, however this pattern is not consistent (Dzus and Clark 1998, Guyn and Clark 1999, Krapu et al. 2000, Amundson and Arnold 2011). Habitats shown to be attractive to early nesting females also can produce higher nest survival rates (i.e., winter wheat; Devries et al. 2008a) and with higher recruitment in early hatched ducklings, advantages from early nesting may convey additional advantages for duckling survival.

My primary objective was to consider the effects of habitat composition on pintail duckling survival rates in cropland-dominated landscapes containing fields sown to winter wheat as compared to grassland-dominated landscapes. I predicted that duckling survival rates would be lower in annual cropland-dominated landscapes. I also tested for survival advantages associated with nesting in winter wheat, including a survival trade-off between higher nesting success in winter wheat offsetting costs of lower duckling survival in croplands and determined if winter wheat conferred survival advantages due to earlier hatch dates as compared to spring-seeded cropland. I predicted that duckling survival would be greater for early hatching birds from winter wheat. Lastly, I considered the relative importance of other factors reported or hypothesized to influence duckling survival, including effects of landscape composition and configuration.

5.2 Study Area and Methods

5.2.1 Study Sites

Work was conducted in the Mixed and Moist Mixed Grassland ecoregions within the Prairie Pothole Region of southern Saskatchewan. The areas are characterized by flat to rolling plains with Solonetzic and Dark-Brown to Brown Chernozemic soils and sporadic glacial till

distributed along hummocky terrain (Fung 1999). I examined two study areas, one each in 2011 and 2012, that were characterized by relatively high pintail breeding pair densities (> 12 pairs/km^2; J.H. Devries, unpublished data) and strong regional landscape gradients ranging from intensive annual crop production with existing winter wheat production to large contiguous tracts of native and tame grasslands (Figure 5.1). Cropland-dominated areas were primarily annual grain, oilseed and pulse crops with lesser amounts of fall-seeded cereals and haylands. Roads and trails were systematically distributed and common, as were active and abandoned farmyards. Perennial cover in cropland areas were primarily restricted to strips of native and non-native mixed grasses located along watercourses, rights-of-way, roadside ditches, steep terrain and larger blocks used as pasture for cattle. Grassland areas contained intact mixed grasslands interspersed with low shrub and sparse trees and low densities of roads and trails. The primary land use was pasture for cattle grazing, with minimal amounts of hay or annual crop production.

In total, 12 study sites were selected from across the two study areas and identified by dominant landscape type (i.e., grassland or cropland). In 2011, sites were located within 48 km of Frontier, Saskatchewan (49° 12' N, 108° 33'W) and consisted of two grassland-dominated ($\overline{x}$ % grassland = 71.6 % and 78.7 %) and four cropland-dominated ($\overline{x}$ % grassland: 25.1 %; range: 4.0 – 47.4 %) sites. In 2012, sites were located within 50 km of Beaubier, Saskatchewan (49° 08' N, 104° 04' W) and consisted of two grassland-dominated (69.9 % and 70.9 %) and three cropland-dominated ($\overline{x}$ % grassland: 11.2 %; range: 5.9 – 16.6 %) sites (Figure 5.1, Table 5.1).

In the year prior to study (i.e., summers of 2010 and 2011) Ducks Unlimited Canada (DUC) staff canvassed landowners for interest in joining a Fall Cereal Crop Habitat Program jointly-funded through DUC and Bayer CropScience. Participating producers agreed to allow access to equal areas of spring-seeded and fall-seeded cereals for nest searching activities. In return, producers were provided with incentive payments to cover seed costs and provide compensation for > 5% crop damage loss due to nest searching (Devries et al. 2008a). Within or near each cropland site, I selected approximately 260 ha of winter wheat and spring-seeded cereals for nest searching. Fall-seeded fields located outside of the study sites were selected if within 4 km of site boundaries and in a similar agricultural landscape. An additional 260 ha of other available cover types also were searched for nests including idle cropland (fallow or cereal stubble), hayland and other perennial cover. At grassland sites, land access was gained through voluntary agreements with landowners with similar acreages of tame and native mixed

grasslands selected for nest-searching. The locations of accessible lands were determined by producers' willingness to participate and individual crop or grazing rotation considerations.

5.2.2 Locating and Monitoring Pintail Nests

I used nest search protocols established by DUC during previous waterfowl nesting studies in the Canadian prairies (Devries et al. 2008a, Howerter et al. 2014). Three nest searches were conducted over 3-week intervals from late April through mid-July, systematically searching all focal habitats. I used all-terrain vehicles towing either a cable or chains (Klett et al. 1986), or a 2.5 cm nylon rope in cropland habitats, to reduce damage to crops (Devries et al. 2008a, Skone et al. 2016). When vehicle use was not possible, a small diameter rope was dragged by hand between two observers on foot. Searches were conducted between 0600 to 1400 hours to increase the probability of female nest attendance (Gloutney et al. 1993) but were not conducted during periods of heavy rain. All upland habitats were searched except for trees, farmyards and flooded wetland vegetation. All searched areas were recorded on aerial photographs.

I recorded the date, time, location (UTM), habitat type, species of attending female, number of eggs and incubation stage (Weller 1956) for each nest, defined as nest bowl with ≥ 1 egg. A small piece of flagging tape was placed 10 m directly north of the nest location to provide reference for subsequent nest visits. To increase sample size and ensure inclusion of early hatched broods, small non-electrified predator-deflection fences (Sargeant et al. 1974) were deployed around pintail nests found in late laying (egg count ≥ 5) or incubation. Approximately 15% and 40% of all pintail nests were fenced in 2011 and 2012, respectively.

5.2.3 Female Capture and Monitoring

I used a stratified random sampling approach, selecting nests for trapping across a range of hatch dates and habitat types. I captured late-incubating females within 4 days of the estimated hatch date using mist nets, and walk-in, spring-loaded or automatic nest traps (Weller 1957, Coulter 1958, Bacon and Evrad 1990, Dietz et al. 1994). I took morphometric measurements (head, keel, and tarsus lengths, ± 1 mm with digital calipers; wing chord, ± 1 mm with a wing board ruler; and body mass, ± 10 g with a Pesola spring scale), a digital photograph of the outstretched right wing and collected the 5th greater secondary covert feather to determine female age. Female age was estimated as second-year (i.e., yearling or SY) or after-second year (i.e.

adult or ASY) based on plumage characteristics, digital photographs and a collection of known–age feathers (Duncan 1985; K. L. Guyn, unpublished data).

Females were marked with an aluminum leg band and equipped with a 4.5 g (2011) or 8.3 g (2012) back-mounted radio transmitter (models A4300 and 4400; Advanced Telemetry Systems, Isanti, MN) attached using prong and sutures (Mauser and Jarvis 1991). To aid identification, a subset of birds (2011: n = 5, 2012: n = 52) received temporary nasal markers (modified from Lokemoen and Sharp 1985). Coloured plastic nasal markers were secured through bird's nares using a short section of mono-filament line, knotted and reinforced with a small amount of cyanoacrylate glue. Following marking, all birds were immediately released onto the nearest wetland. All capture and handling protocols were approved under University of Saskatchewan Animal Care Committee standards (no. 20110039), and scientific research permits (nos. 12FW118, 11-SK-SC013, and 10458D).

Immediately prior to the estimated hatch date, the predator deflection fence was raised (approx. 15 cm) off the ground to allow females to lead newly hatched ducklings from the nest unimpeded. Nests were visited immediately post-hatch to determine initial brood size (Orthmeyer and Ball 1990). Using a vehicle-mounted null array telemetry antenna or handheld system (Kenward 2000), brood rearing females were tracked every 1 to 7 days between hatch and 30 days post-hatch or until total brood loss, female mortality or radio-failure was confirmed. I attempted to count ducklings immediately following hatch to determine brood size following initial movement, then weekly or opportunistically thereafter until tracking ceased. For females that were not located during regular radio tracking, I conducted weekly scans for missing signals as well as two expanded searches of the study area using fixed-wing aircraft in each year.

Duckling counts were made using passive observation from a distance ($\overline{x}$ distance: 88.3 m) using spotting scopes or binoculars to reduce disturbance and count error. During each observation, I verified female identity (i.e., nasal marker, radio antenna visible, appropriate age of young, etc.) and recorded the number and age of ducklings and whether the count was considered complete (i.e., all ducklings visible), partial (observer uncertain if all ducklings had been observed) or mixed (brood consisted of ducklings of different ages or species). If a female was suspected of losing a brood, or a partial count was obtained (e.g., females using ponds with dense vegetation), I made multiple observation attempts to confirm brood size or loss and when

30 days old, I performed active counts (i.e., brood drives) to confirm final brood size. I assumed total duckling loss if females abandoned broods prior to ducklings reaching 30 days in age. Incomplete counts and incorrect assumptions about duckling mortality following abandonment may bias survival estimates low if ducklings survive without detection or when orphaned (Clark et al. 2005) but there is no reason to expect any systematic biases in these detection problems among landscapes and habitats that would affect my results.

5.2.4 Brood Movement and Habitat Classification

Locations and error ellipses of radio-marked females were calculated using LOAS™ (Ecological Software Solutions LLC, Hegymagas, Hungary) and cross-referenced to field maps and observation records. As triangulation provides only an estimated location, I followed Bloom et al. (2012) and assigned hen locations that occurred in or near wetland habitat (i.e., as determined by error ellipses) to wetland centroids if ponds were < 5 ha, or to the estimated or observed location when ponds were > 5 ha. To account for temporary female movements away from broods to rest or feed (i.e., brood breaks; Talent et al. 1983), locations were excluded from analysis when females left ponds with confirmed brood presence for one tracking session but returned to the original location and the brood was subsequently re-sighted. Large or frequent movements of females can occur following complete brood loss so I right-censored locations for females suspected of complete brood loss to the last known location where the brood was sighted or where the female spent >1 day prior to brood loss. I also excluded two females whose broods failed to leave the nest.

I created apparent female travel routes by connecting nest, female and brood locations based on straight line movements in the Spatial Analyst extension of ArcGIS 10.2 (Environmental Systems Research Institute, Inc. [ESRI], Redlands, CA). Straight line movements oversimplify both travel distance and habitat use as habitats used outside of tracking sessions are missed. Because duckling survival typically increases with duckling age (Guyn and Clark 1999, Pietz et al. 2003, Amundson and Arnold 2011, Bloom et al. 2012), I followed Bloom et al. (2012) and divided brood routes into areas used during two age periods (≤ 7 days or >7 days old). Each route was buffered by 700 m, a distance selected based on the average movement distance between pintail nests and first recorded wetland location (mean = 691 m). The buffered area was used to calculate age-specific habitat composition and configuration metrics for each brood.

I determined upland habitat type within each study site plus a 3.2 km buffer based on: 1) ground observations conducted in late July; 2) panchromatic satellite images (2.5 m resolution) taken between June and July; and 3) high-resolution satellite imagery (0.5 m) taken within two years of the study period. I classified uplands based on dominant land cover and land use, including but not exclusive to annual cropland (e.g., spring cereal, fall cereal, oilseed, stubble or idle), perennial vegetation (native grassland, tame grassland, hay, trees, or shrubs), wetland (temporary, seasonal or semi-permanent ponds; Stewart and Kantrud 1971) or human infrastructure (e.g., farmyard, road, ditch), as per Bloom et al. (2012) and Howerter et al. (2014). Habitat maps were created in ArcGIS.

5.2.5 Model Covariates and Predictions

Model covariates were selected based on habitat and landscape factors shown or hypothesized to influence survival across a variety of scales. Grassland-dominated landscapes contain higher pintail nest densities and nest survival rates compared to cropland-dominated landscapes (Richkus 2002, Kowalchuk 2012); however, high proportions of perennial cover have been associated with lower mallard duckling survival (Amundson and Arnold 2011). Dominant landscape type was categorized both qualitatively and quantitatively and, based on patterns in previous studies, I predicted that duckling survival would be greatest in grassland-dominated landscapes. Localized habitat composition surrounding ducklings during brood-rearing may also influence survival. In addition to effects of perennial cover stated (see above), the abundance of flooded wetland basins (i.e., ponds) is also positively associated with duckling survival, particularly for seasonal wetlands (Dzus and Clark 1998, Gendron and Clark 2002, Amundson and Arnold 2011, Bloom et al. 2012, Howerter et al. 2014). I examined relationships between duckling survival and relative habitat composition within age-specific brood buffers (days 0 to 7 and 8 to 30). Furthermore, I tested for effects of nesting habitat type and specifically, enhanced survival in fall-seeded crops which may indirectly benefit early hatched ducklings (Devries et al. 2008a, Skone et al. 2016). Overall, I predicted that higher proportions of grassland, perennial cover, fall-seeded croplands and seasonal wetlands would improve duckling survival.

Spatial configuration of habitat may influence waterfowl nesting success through habitat fragmentation or edge effects as nest predators commonly forage along wetland edges (Phillips et al. 2003). Pintails also nest further from water compared to other waterfowl species (Duncan 1987) and ducklings may be more vulnerable to predation during overland moves (Rotella and

Ratti 1992a, Guyn and Clark 1999). Fragmentation is the dissection of habitat into spatially divided parts that occurs separately from habitat loss (Villard et al. 1999, Villard and Metzger 2014, Wang et al. 2014). To determine if landscape configuration influences duckling survival, I derived indices of relative proximity and fragmentation for both grassland and wetland habitats. For each brood age-specific buffer, I calculated the density of seasonal ponds and estimated proximity of grassland and wetland patches by summing the patch area-to-distance ratios for each habitat type (Bender et al. 2003). I calculated multiple fragmentation indices for both grasslands and wetlands, including the density of edges and back transformed residuals of total edge length and percentage of habitat type. I also used the total number of grassland patches, excluding edges along the outer buffer bounds.

Early hatching dates often have positive effects on duckling survival (Dzus and Clark 1998, Guyn and Clark 1999, Krapu et al. 2000, Amundson and Arnold 2011; but see Gendron and Clark 2002). Relative hatch date was calculated from the date of the first predicted hatch date for all pintail nests within each year (28 May 2011 vs. 25 May 2012). Birds which breed earlier maximize the period available for duckling growth prior to fall migration, usually encounter greater wetland densities (Dzus and Clark 1998) or may experience lower mortality risk if predators are not yet actively foraging for waterfowl nests or broods (Grand and Flint 1996). I therefore predicted that earlier hatch dates would be associated with higher duckling survival. To partially account for duckling age effects, I considered an age-based model as the biological baseline from which to evaluate additive landscape, habitat and fragmentation covariates. I also considered year as a categorical grouping variable to account for potential spatiotemporal variation in duckling survival. A description of all covariates and predictions is outlined in Tables 5.2 and 5.3.

5.2.6 Duckling Survival Models

I estimated cumulative duckling survival over a period of 30 days (ϕ^{30}) using the nest survival module in Program MARK (Rotella et al. 2004, Dinsmore and Dinsmore 2007) implemented through the RMark package (Laake 2013) within Program R (R Core Team 2015). I used generalized linear models with a logit link and binomial error distribution to bound estimates between 0 and 1 and estimated daily survival rate (DSR) as a function of both time varying and fixed covariates using;

$$DSR_{ji} = \frac{exp^{(\beta_o + \sum_j \beta_j X_{ji})}}{1 + exp^{(\beta_o + \sum_j \beta_j X_{ji})}} \quad (5.1)$$

where DSR_{ji} is the daily survival rate for the *j*th covariate on ith day, β_o is the intercept, β_j are covariate coefficient and X_{ji} are covariate values (Rotella et al. 2004). As ducklings were not observed daily I could not determine exact dates of duckling mortality; however, the nest survival module provides a flexible manner to account for such uncertainty. Five inputs of data are required: *i)* first day ducklings are present (hatch = day 1); *ii)* last day confirmed alive; *iii)* last day visited; *iv)* fate (alive = 0, dead = 1); and *v)* number of individuals in each record. For example, if 5 ducklings hatch from a nest (day 1) and are seen one week later (day 8) but only 3 are counted during the following week (day 15), then 2 ducklings would have the following row of data: last day present = 7, last day visited = 15, fate = 1, and number of individuals = 2. The remaining 3 individuals would be monitored until another mortality event or ducklings reached 30 days' post-hatch (day 31). Therefore, multiple ducklings are represented by a single row of data.

Several assumptions are made with this approach, including: 1) ducklings are aged accurately; 2) all observations are recorded; 3) observations do not influence survival; 4) fate is correctly assigned; 5) homogeneity of DSR; and 6) fates are independent. To meet these assumptions, I used established data collection protocols with passive observation, excluded partial or mixed counts, right censored broods when fate was unknown or past 30 days of age, and included a wide range of covariates to model heterogeneity in the data. I was unable to measure model goodness-of-fit as no method is available for the nest survival package in RMARK at this time (Dinsmore et al. 2002, Walker et al. 2013). Duckling fates are likely non-independent (e.g., brood-mates have similar fates) so I estimated over-dispersion ($\hat{c}$=2.99) using program MARK and 5,000 bootstrap simulations of a model containing duckling age and study site effects (Amundson and Arnold 2011, Skone et al. 2016).

I compared models using Akaike's Information Criterion adjusted for sample size and overdispersion ($QAIC_c$; Burnham et al. 2002) and ranked models based on the relative difference in $QAIC_c$ relative to the best-approximating model ($\Delta QAIC_c$). I considered models ≤ 2 $\Delta QAIC_c$ units as highly competitive; however, as adding additional model parameters can decrease $\Delta QAIC_c$ without adding useful information (i.e., uninformative parameters; Arnold 2010), I only

considered models to be competitive if parameters in the top model were not a subset of those in competitive models (Devries et al. 2008a). I report standard error for coefficients and predictions with derived 85% confidence intervals around the ϕ^{30} survival estimates using Markov chain Monte Carlo simulations (Amundson and Arnold 2011).

I used a multi-stage approach to model duckling survival; a biological baseline model (duckling age and year effects) was established followed by consideration of both habitat composition and configuration effects across scales – landscapes (study site) to local environments (nesting and brood-rearing habitat). Candidate baseline models included an intercept-only model (i.e., statistical null; DSR_{Null}) and three age-based models: *i)* ≤7 and >7 days old ($DSR_{1\text{-}7d,\ 8\text{-}30d}$; Bloom et a. 2012); *ii)* weekly survival (DSR_{Week}); and *iii)* continuous logistic function of age (DSR_{Age}; Amundson and Arnold 2011). A full age-dependent model (i.e., daily survival) was not considered due to potential for over-parameterization. The intercept-only model ($QAIC_c$ = 736.69, -2 Log-Likelihood = 2196.7) had the lowest support throughout all stages and was excluded from model tables.

To the baseline model, I incorporated covariates of interest for each spatial scale. Because multiple covariates were likely correlated measures of the same environmental attribute (e.g., landcover as percent grass or percent crop, proximity vs. fragmentation, etc.), I calculated Pearson correlation coefficients for all covariates prior to modelling and did not incorporate related covariates in the same model when correlation values were > |0.4|. Correlated covariates were represented individually as competing hypotheses and the best covariate from each pair was selected to build subsequent models. Due to limited sample sizes, I only considered additive effects, a maximum of three covariates of interest (excluding the intercept and duckling age terms), and *a priori* hypotheses rather than testing all combinations. I also used separate estimates of composition for each age-specific buffer (0 – 7 days and 8 – 30 days). Full model tables are presented in Appendix C.

5.3 Results

5.3.1 Site-level

In 2011, over 4,500 ha of upland habitat was searched for nesting waterfowl with 43.4% of the searched area classified as grassland, 16.8% as spring-seeded cropland, 15.3% fall-seeded cropland, and 24.5% idle cover or hayland. In 2012, nest searching was conducted on 4,050 ha,

36.9 % of which was in grassland, 15.1% in spring-seeded cropland, 19.3% fall-seeded cropland, and 28.6% idle cover or hayland. In total, 342 northern pintail nests were found, and 104 attending females were captured and radio-marked across a range of hatch dates (relative mean ± S.E.) in each year (2011: 46.5 ± 2.8 days, 2012: 26.4 ± 2.1 days; see Figure 5.2). One study site in 2011 was excluded from analysis due to small sample size of broods (n = 2) and a lack of winter wheat. Data censoring of missing females or with unknown brood fates resulted in survival histories for 41 broods (262 ducklings) in 2011 and 47 broods (346 ducklings) in 2012 and resulted in an effective sample size of 7,964 exposure intervals. Descriptive statistics for modeled variables are provided in Table 5.3.

5.3.2 Landscape-level

The top-ranking baseline model of duckling survival included a linear trend of duckling age (Table 5.4A; Figure 5.3). The addition of a site-year covariate did not result in a reduction in $QAIC_c$ and was not considered further. The best-approximating model incorporating landscape-level (i.e., study site) covariates included a strong effect of dominant landscape type (grass: β = 0.164 ± 0.011) and relative hatch date (β = 0.013 ± 0.003), in addition to duckling age (β = 0.953 ± 0.141; Table 5.4B). After accounting for hatch date effects, ϕ^{30} duckling survival rate was 27.4 % in cropland-dominated compared to 45.2 % in grassland-dominated sites (Figure 5.4).

5.3.3 Nesting Habitat and Trade-offs

The best-approximating model examining effects of nesting cover type on pintail DSR included covariates of age (β = 0.164 ± 0.011), relative hatch date (β = 0.222 ± 0.058) and nest habitat type (annual crop: β = -0.719 ± 0.135; fall crop: β = -0.073 ± 0.144; Table 5.4C). Cumulative ϕ^{30} rates were comparable between perennial cover (40.8%) and winter wheat (38.2%) and ducklings from nests in spring-seeded cropland had the lowest survival rates (16.9%) when age and hatch date were held at their mean (Figure 5.5). I did not find support for subdivision of habitat type within either perennial cover or annual cropland. For broods originating only from spring-seeded cropland (n = 11) or winter wheat (n = 21), the best-approximating trade-off model included only age (β = 0.139 ± 0.18) and hatch date (β = 0.431 ± 0.11). The addition of winter wheat (β = 0.430 ± 0.19) had a positive effect on survival but did not improve model fit (Δ $QAIC_c$ = 0.40; Figure 5.6).

5.3.4 Local Landscape Configuration and Composition

The abundance and arrangement of wetlands surrounding broods contributed to variation in pintail duckling survival rates (Table 5.5). In addition to age effects ($\beta = 0.170 \pm 0.011$), the top-performing model for habitat effects measured at the brood-route scale contained the proportion of seasonal wetlands ($\beta = 0.025 \pm 0.004$), proportion of perennial cover ($\beta = 0.006 \pm 0.001$) and the density of wetland edges ($\beta = -0.002 \pm 0.000$). Higher proportions of seasonal wetlands and perennial cover had positive survival effects, while higher densities of wetland edge had a negative effect on survival (Figure 5.7).

5.4 Discussion

5.4.1 Landscape Differences

Results matched my initial prediction that cumulative 30-day survival is lower in cropland-dominated landscapes relative to grassland-dominated landscapes. The 45% survival estimate for grassland landscapes was within the range reported for a large managed wetland complex in grasslands of southern Alberta (42 – 65%; Guyn and Clark 1999) and higher than the Yukon-Kuskokwim Delta in Alaska (4 – 14%; Grand and Flint 1996). The cumulative survival estimates for cropland landscapes (27%) also was comparable to another study of pintail duckling survival conducted in southern Saskatchewan (29%; Peterson 1999). My estimates also are within the range of duckling survival estimates reported in other similar species within the PPR (Talent et al. 1983 [35%], Rotella and Ratti 1992b [22 %], Amundson and Arnold 2011 [16-26 %], Howerter et al. 2014 [24-67%]).

Grassland-dominated landscapes likely represent the ecosystem in which pintails would have evolved, whereas cropland-dominated landscapes are a more recent landscape feature that pintails may not yet have fully adapted to. Devries et al. (2018) showed that pintail nest habitat selection in prairie landscapes was dynamic, varying with breeding density and by landscape features; they also found that nesting pintails had high selection for idle grass and more neutral responses for cropland. Kowalchuk (2012) investigated differences in nesting ecology across a landscape gradient in southern Alberta and reported higher breeding densities and nesting success for pintails in grassland-dominated compared to cropland-dominated landscapes. These results and conclusions are reinforced by my findings which more comprehensively demonstrate offspring survival benefits for pintails breeding in grassland-dominated landscapes.

In contrast to Amundson and Arnold (2011), I found that site-specific habitat composition (e.g., percent wetland, percent grassland) did not play a more important role than the overall landscape type. This may suggest that multiple attributes influence survival of pintail ducklings. Grassland-dominated sites had greater wetland densities relative to cropland sites, which are likely a consequence of both geography, soil type and cultivation suitability. Grassland landscapes also are less heavily influenced by anthropogenic features such as farmyards, roads, shelterbelts and likely support different predator communities (Sargeant et al. 1993). Dominant patterns in brood rearing habitat and/or duckling predator communities would be difficult to determine due to the confounded site-year effect and visiting each site only once. Teasing apart how wetland conditions change or differences in predator communities may provide additional insights into the most influential factors present in these landscapes that I was unable to measure. For example, cropland landscapes in 2011 were more diverse in the amount of grassland (Table 5.1), yet year was not an important factor. Therefore, subtle differences in landscape composition may not have detectable effects on survival and habitat composition may play a larger role at more localized scales.

5.4.2 Nesting Habitat Differences

This study is the first to demonstrate the effects of fall-seeded crops on pintail duckling survival, where estimates for broods originating from perennial cover (41 %) were similar to those from winter wheat (38 %) and where both had greater survival rates than broods hatching within annual croplands (17 %), including spring-seeded crop and stubble. These results are like nesting studies where fall-seeded crops have higher nest survival rates relative to spring-seeded crops (Devries et al. 2008a) or even perennial cover (Skone et al. 2016). My results suggest that nesting habitats may confer survival benefits to ducklings during the early post-hatching period. As in the landscape-scale analysis, the type of habitat type played a more influential role vs. the amount of coverage (i.e., percent perennial cover). This differs from Skone et al. (2016) who reported that nest success declined with higher percentages of wetlands and cropland.

Although managed hayland and perennial cover provide benefits to nesting waterfowl, the provision of early overhead nesting cover and safe refuge from spring seeding operations is hypothesized to be a key driver for enhanced nest success in fall-seeded croplands (Devries et al 2008, Skone et al. 2016, Duncan and Devries 2018). In contrast, annual cropland environments provide sparse coverage and may increase the risk of nest predation, the major contributor to nest

loss for waterfowl in agricultural landscapes. Yet evidence for overland mortality of ducklings between nests and wetlands is uncertain and difficult to obtain across species or regions (Dzus and Clark 1997, Guyn and Clark 1999, Gendron and Clark 2002, Bloom et al. 2012). If fall-seeded crops provide not only overhead cover for nests but buffering cover for brood-rearing wetlands during initial movements to wetlands, then this could explain survival benefits. This study also occurred during a wet period of prairie drought cycles, with abundant pond habitat within or near winter wheat fields. Investigations into the benefits or trade-offs of fall-seeded crops during drought conditions or in low wetland density landscapes would provide valuable additional information for waterfowl habitat managers.

5.4.3 Trade-offs of Nesting in Winter Wheat

Over half of the mixed-grass prairie in Saskatchewan has been lost to cultivation and continues to see some of the highest conversion rates within the Great Plains of North America (Gage et al. 2016). Prairie breeding waterfowl will increasingly encounter nesting areas dominated by spring-seeded cropland and, as pintails select these habitats proportionate to their availability (Richkus 2002, Devries et al. 2018), ever larger segments of the pintail population will breed in cropland-dominated landscapes. Results from this study show that pintail duckling survival was lower in cropland-dominated than in grassland-dominated landscapes, and particularly low for ducklings hatched from nests in spring-seeded cropland. When combined with the reported low nest survival rates in this habitat type (Richkus 2002, Devries et al. 2008a, Devries et al. 2018), pintails are at risk for low reproductive success in the intensively farmed areas now characterizing most of the PPR (Zhao et al. 2019). However, fall-seeded cropland provides benefits in terms of nest (Devries et al 2008a) and duckling (this study) survival, implying that use of winter wheat could enhance pintail reproductive success. Yet, the question remains: are benefits of higher nesting success in winter wheat enough to offset costs of lower duckling survival in intensively farmed landscapes?

To determine if winter wheat confers greater survival advantages relative to spring-seeded croplands I combined results from this study with reproductive values reported in the literature to estimate the number of fledged pintails that could be expected from identical acreages of spring-seeded cropland compared to winter wheat (assuming equivalent effects of hatch date, female quality and wetland characteristics). I used a combination of reported habitat specific nest density and survival rates (Devries et al. 2008a, 2018), hatched nest densities

(Skone et al. 2016), mean clutch size (Duncan 1986, Guyn and Clark 1999, Richkus 2002) as well as mean brood size and cumulative 30-day survival rates reported in this study (Figure 5.6). As prevalence of winter wheat is not expected to be equivalent to spring-seeded crops, I then scaled these estimates to represent a typical landscape (Table 5.6).

Survival estimates in each habitat type ranged widely but estimates indicated that winter wheat could produce over 5 times the number of ducklings relative to spring-seeded cropland. To estimate the number of fledged young per ¼ section or study site, I used a range of published values of nest density, nest and brood survival and average sizes of clutches and broods. I did not correct for seasonal declines in clutch size or differences in wetland densities, both known factors to influence brood size and survival. Based on these calculations (Table 5.6) winter wheat initially produces greater numbers of hatched nests, likely a consequence of elevated nest density and survival while enhanced duckling survival maintains these nesting gains. I did not find evidence to support a strong trade-off supressing nest survival benefits of winter wheat by low duckling survival in cropland-dominated landscapes. While duckling survival rates in cropland-dominated landscapes are lower than grassland-dominated landscapes, survival estimates for cropland-dominated areas in this study were boosted by winter wheat. An even larger difference between landscape types would be expected if winter wheat had not been present. Currently, the typical PPR landscape contains very little fall-seeded cropland and this study highlights that increases in winter wheat has high potential for enhancing pintail productivity in the agricultural landscapes of prairie Canada.

5.4.4 Effects of Female Attributes

Older ducklings had higher survival rates relative to younger ducklings, a result consistent with other studies of pintails in both prairie and arctic environments (Grand and Flint 1996, Guyn and Clark 1999) as well as other species within the PPR (Pietz et al. 2003, Amundson and Arnold 2011, Howerter et al. 2014). The linear age trend in duckling survival appeared to level off near 10 – 14 days in age (Figure 5.3), matching results from other studies (Grand and Flint 1996, Guyn and Clark 1999). Increasing survival with age is likely a factor of ducklings becoming increasingly independent and less vulnerable to predation (Pearse and Ratti 2004, Amundson and Arnold 2011) and/or cold and inclement weather (Krapu et al. 2000, Amundson and Arnold 2011, Bloom et al. 2012).

Hatch date also was identified as an important covariate at both the landscape and nest site scales, although it did not appear in the top model for local environments. The positive hatch date results were opposite to other pintail studies (Grand and Flint 1996, Guyn and Clark 1999) where pintail duckling survival decreases over the nesting season. The difference between this study and others may be due to site-specific differences. In this study, duckling survival increased as the season progressed which may be a result of increased food availability or emergent vegetation in wetlands which would provide both food and concealing cover for ducklings. In most wetlands within my study areas, the amount of open water in each wetland could decrease dramatically due to water loss and rapid infill of *Elocharis, Carex* and *Polygonum* plant species. Heavy plant cover not only inhibited duckling exposure to observers but to potential predators and inclement weather as well. Weather patterns in the PPR early in the season also can expose broods to rain and cold winds with greater variability in air temperature and precipitation (Krapu et al. 2006, Howerter et al. 2014). The presence of a later spring or variable weather could have disproportionately reduced survival of newly hatched ducklings and may have skewed my results. It also is possible that very low early survival coupled with higher survival among mid-season broods, as reported by Blums et al. (2002), produced an increasing seasonal pattern observed in pintails although I found no nonlinear relationship between survival and hatch date.

The lack of a hatch date effect at in the local scale analysis was an unexpected result. Localized upland and wetland habitats are likely to have greater influences on duckling survival as compared to broader landscape conditions. If localized habitat conditions for both wetland and upland habitat were dominant factors determining duckling survival, then specific tests of interactions between habitat type and hatch date may be useful. However, limited sample sizes and combined site-year effects were a restricting factor for this analysis. Local habitat conditions also were measured at a single point in time and would not represent change across time. For example, broods utilizing a local landscape early versus late in the season may have differential survival, but the lack of this effect suggests that habitat composition, rather than configuration, played a larger role. Further work with larger number of broods and sites would provide greater insight into these effects.

5.4.5 Effects of Brood Route Habitat

Landscape composition and fragmentation were important determinants of duckling survival. Ducklings inhabiting areas with greater proportions of perennial cover had higher cumulative survival rates (Figure 5.7). This result matched my prediction and was consistent with patterns from the larger scale analyses in my study. However, studies of mallard ducklings have found opposite patterns where perennial cover had negative influences on duckling survival and speculated that these were driven by differences in predator communities (Amundson et al 2011, Bloom et al. 2012). Bloom et al. (2013) also examined habitat selection at finer scales and discovered negative effects of shrub and tree habitats. In the Parkland region of the PPR, trees and shrubs are more common than the southern grassland landscapes studied here. Avian predators would have had fewer nesting and perching opportunities and the large intact grasslands support lower abundance and different predator communities relative to agricultural landscapes (Ball et al. 1995). However, I did not index predator abundance and cannot ascertain whether this explanation is tenable.

The amount of seasonal wetland habitat near broods was positively correlated with duckling survival (Figure 5.7). This result also matched my prediction and is largely consistent with studies of wetland effects on duckling survival within the PPR (Rotella and Ratti 1992b, Krapu et al. 2006, Amundson and Arnold 2011, Bloom et al. 2012). Abundant seasonal wetlands often are used by brood-rearing waterfowl, providing concealing cover, shallow feeding zones and abundant, nutritious invertebrate food supply for growing ducklings (Cox Jr. et al. 1998, Twining et al. 2016). Bloom et al. (2013) examined how mallard habitat selection during brood-rearing and found that at study site scale females selected areas with more seasonal wetlands. Both Krapu et al. (2000) and Amundson and Arnold (2011) reported higher duckling survival estimates with increasing wetland density and abundance. However, similar to the grassland effect above, it is hypothesized that brood predators like American mink (*Neovison vison*) heavily use semi-permanent and permanent waterbodies (Arnold and Fritzell 1990, Krapu et al. 2004) which may reduce duckling survival in these habitats. This result also is consistent with waterfowl nest survival studies where variation in nest success within the PPR was partially explained by predator presence rather than pond density. Drever et al. (2004) and Dzus and Clark (1998) found that seasonal declines in pond abundance interacted with hatch date to supress duckling survival at lower pond abundances.

This study is the first to demonstrate that duckling survival is influenced by the spatial configuration of proximate brood habitats as the best-approximating survival model at the local-scale included the relative amount of wetland edge which had a negative effect on duckling survival (Figure 5.7). As highlighted above, wetland abundance is consistently an important factor influencing multiple determinants of waterfowl reproductive success (Rotella and Ratti 1992b, Austin 2002, Podruzny et al. 2002, Krapu et al. 2006, Amundson and Arnold 2011, Bloom et al. 2012) yet no studies that I am aware of have examined for edge effects, patch size or connectivity. Studies of nest success can provide insight into the role for edge effects. A classic example found rates of depredation for tree nesting songbirds were susceptible to edge effects (Yahner and Scott 1988) as arboreal nests were depredated at higher rates in edge habitats compared to interiors. In grasslands, Stephens et al. (2005) found a curvilinear effect where waterfowl nest survival was lowest at intermediate levels of grassland fragmentation and nest success declined with increasing wetland density. Horn et al. (2005) also found low survival in intermediate grassland patches but these patterns may not be consistent for all species as nesting dabbling ducks may respond to separate landscape features and scales (Koper and Schmiegelow 2006) and Pasitschniak-Arts et al. (1998) found that waterfowl nest predation risk was not related to distance from edge but instead overall habitat type. These results suggest that diverse predator communities are found in moderately fragmented landscapes and can drive nesting success for ground nesting birds, which may also have implications for offspring survival.

In this study the relative amount of wetland edge was more important that grassland edge and fragmentation, resulting in a negative association with duckling survival. Wetland edges provide vital brood-rearing habitats with shallow water areas and abundant vegetation supplying food and shelter for ducklings. Yet the interface between terrestrial and aquatic habitats may also increase predation risk as common prairie predators of waterfowl nests and broods preferentially select wetland and edge habitats in both grassland and cropland-dominated landscapes (Fritzell 1978, Arnold and Fritzell 1990, Larivière and Messier 2000, Phillips et al. 2001, Phillips et al. 2004). Broods that used areas with a greater abundance of small wetlands or complex shorelines would have relatively more wetland edge compared to broods that used a single large wetland. While the use of residuals from a regression of edge and wetland area should reduce confounding effects between fragmentation and habitat amount, wetland type may also play a role. The PPR is characterized by round pothole-like wetlands and if the presence of complex

edges is associated with larger and more permanent waterbodies then habitat type may contribute to edge effects. In this study I did not test for nonlinear edge effects of fragmentation or measure differences in predator communities or predation risk. Future studies which record individual wetland characteristics throughout brood rearing as related to predation events would provide enhance detail to further inform these relationships.

Several factors could determine why additional fragmentation and configuration metrics did not influence survival. Landscape ecologists often rely on configuration metrics to explore how landscape arrangement influences biological function. While edge effects are shown to influence nest survival, mobile broods that use both uplands and wetlands may not be ideal for examining the effects fragmented habitats and edge-effects as defining a habitat or its edge relative the surrounding matrix becomes challenging. The determination of where mortality occurs in relation to habitat edges would also improve insights into edge effects in this system where studies examining detailed movement and habitat use would provide novel insight into where ducklings are exposed to predation. I did not find an effect of patch size or proximity and this could indicate that pintail broods are not influenced by changes in the spatial arrangement of habitats or, alternatively, that the scale of analysis does not align with the driving forces (Stephens et al. 2004, Fahrig 2013). If predator abundance is the main factor that influences duckling survival then we would not expect that spatial configuration metrics would be supported unless the arrangement or scale of influence for predators was biologically relevant (Debinski 2006, Prevedello and Vieira 2010).

Continued grassland loss is one of the greatest threats to not only northern pintail populations in the prairies but many other grassland bird communities as well. Increasing commodity prices and demands for land dedicated to crop production will continue to place pressure on the retention of remaining native prairie and associated wetlands. Seasonal wetlands provide essential habitat for brood-rearing waterfowl and their purposeful drainage during periods of drought and cultivation could have lasting impacts to habitat quality and capacity (Bartzen et al. 2010). Results from this study highlight the importance of retaining grassland-dominated landscapes, with abundant native prairie and perennial cover and suitable wetland capacities that enable successfully brood-rearing. These landscapes also are often valued from multiple perspectives and for broader conservation objectives, however, an underutilized tool that could benefit waterfowl across broader regions of the PPR is the expansion and promotion

of winter wheat in agricultural landscapes. Results from this study highlight the gains in pintail productivity that may result with even moderate deployment of fall-seeded crops into areas with suitable brood-rearing habitats. In this way, pintail conservation and productivity in the PPR would benefit from increased adoption of winter wheat, with gains only amplified when favorable brood-rearing landscape are targeted for deployment of winter wheat for conservation purposes. This study demonstrated the ability for fall-seeded cropland to benefit waterfowl productivity and may provide an important avenue to enhance waterfowl habitats across the PPR.

Table 5.1. Landscape composition (% of area) and number of northern pintail broods monitored on 11 study sites used to evaluate duckling survival in Saskatchewan, 2011 – 2012. Each site was studied for one year only. Upland habitat types include: Grass – native and tame species primarily found in pastures, road right-of-ways and riparian areas; Hay – grasses and legumes seeded and cut annually for hay; Fall – annual cereals seeded in the fall (e.g., winter wheat); Spring – annual crops seeded in the spring (e.g., wheat, barley, canola) or lands previously seeded but left idle (e.g., stubble, fallow). Wetlands were classified by vegetation type, water depth and water permanency (see Stewart and Kantrud 1971).

Year	Landscape	Site	Broods (n)	Area (ha)	Perennial Cover		Cropland		Wetland Basins	
					Grass	Hay	Fall	Spring	Seasonal	Semi-permanent
2011	CROP	BRA	9	4,221	43.8 %	9.7 %	3.7 %	30.1 %	2.4 %	3.7 %
		SHA*	9	4,205	47.4 %	7.5 %	0.0 %	16.2 %	2.5 %	4.8 %
		TURn	5	4,201	4.0 %	0.1 %	5.4 %	42.2 %	2.0 %	11.7 %
		TURs	6	4,242	5.1 %	0.0 %	1.3 %	31.8 %	4.3 %	10.3 %
	GRASS	ROB	9	4,220	78.7 %	0.0 %	0.0 %	0.0 %	8.9 %	10.7 %
		WIL	3	4,215	71.6 %	8.4 %	0.0 %	4.5 %	3.8 %	6.4 %
2012	CROP	OUN	11	6,505	11.0 %	7.8 %	8.6 %	58.1 %	2.7 %	8.2 %
		RAD	7	6,560	16.6 %	6.1 %	9.5 %	58.0 %	1.7 %	3.4 %
		RAT	5	6,551	5.9 %	2.3%	12.1 %	66.9 %	1.5 %	7.7 %
	GRASS	ALM	14	6,524	70.0 %	4.3 %	0.0 %	8.5 %	7.8 %	8.0 %
		MIN	9	6,599	71.0 %	2.3 %	0.0 %	15.8 %	2.5 %	6.6 %

* Three brood-rearing females were radio-marked in areas outside the SHA site in 2011. The outer area was selected due to availability and access to winter wheat.

Table 5.2. Covariates of interest for *a priori* and exploratory models explaining variation in northern pintail duckling survival rates in southern Saskatchewan, 2011 – 2012. Predicted responses (model β's) are displayed as positive (+), negative (-) or neutral (±) effects. All exploratory covariates (*italics*) measure landscape configuration at the brood route scale and have unique values for each age class (≤ 7 days or > 8 days post hatch).

Scale	Variable	Definition	Predicted Response
All	AGE	Duckling age	+
	HD	Hatch date (relative)	−
	YR	Year of study (confound with study area/site)	±
Study Site	LAND	Dominant land use (grassland, cropland)	+
	GRSS	Proportion of study area that is grassland	+
	PCVR	Proportion of study area that is perennial cover	+
	CROP	Proportion of study area that is spring-seeded cropland	+
	WETL	Proportion of study area that is wetland	+
	WET3	Proportion of study area that is seasonal wetland	+
	WET4	Proportion of study area that is semi-permanent wetland	±
Nest	HAB	Nesting habitat: perennial cover (grass, or hay), cropland (spring-seeded or idle) or winter wheat	±
Brood Route	*PGR*	Proportion of buffer that is grassland	+
	PPC	Proportion of buffer that is perennial cover	+
	PSS	Proportion of buffer that is spring-seeded cropland	−
	PWW	Proportion of buffer that is winter wheat	+
	PWT	Proportion of buffer that is wetland	+
	PW3	Proportion of buffer that is seasonal wetland	+
	PW4	Proportion of buffer that is semi-permanent wetland	±
	FRG	Fragmentation of grassland habitat	−
	EDG	Edge density of grassland habitat (m/ha)	−
	ERG	Grassland edge index (residuals)	−
	PXG	Proximity of grassland patches	+
	WTD	Wetland density (n/km^2)	+
	EDW	Edge density of wetland habitat (m/ha)	−
	ERW	Wetland edge index (residuals)	−
	PXW	Proximity of wetlands	+

Table 5.3. Descriptive statistics for the multiscale analysis of pintail duckling survival with covariates of interest measured at the scale of females (i.e., brood) and brood routes (in two periods: hatch to 7 days post-hatch and day 8 to fledge). Mean ± SE (range) are displayed for brood-rearing northern pintails monitored at study sites in southern Saskatchewan, 2011 – 2012. Descriptive statistics for landscape level variables (i.e., study site) are described in Table 5.1 and descriptions of model variables are found in Table 5.2.

Scale	Variable	Brood Age			
		Days 0 -7		Days 8 -30	
Hen	HD		35.6 ± 2.0	(1 – 76)	
Brood Route	PGR	50.8 ± 4.4	(0 – 100)	33.2 ± 4.4	(0 – 100)
	PPC	56.5 ± 4.3	(0.5 – 100)	36.1 ± 4.5	(0 – 100)
	PSS	31.9 ± 3.6	(0 – 100)	18.9 ± 3.4	(0 – 98)
	PWW	9.8 ± 1.8	(0 – 76)	4.1 ± 1.3	(0 – 70)
	PWT	13.3 ± 1.1	(1 – 53)	10.1 ± 1.4	(0 – 88)
	PW3	25.4 ± 1.8	(0 – 62)	13.8 ± 1.8	(0 – 70)
	PW4	62.9 ± 2.6	(0 – 98)	41.2 ± 4.0	(0 – 96)
	FRG	-0.0 ± 0.1	(-2 – 2)	-0.0 ± 0.1	(-3 – +3)
	EDG	473.4 ± 66.4	(17 – 2590)	197.6 ± 42.2	(0 – 2540)
	ERG	0.0 ± 0.03	(-0.9 – 0.6)	-0.01 ± 0.02	(-1.2 – 0.6)
	PXG	0.3 ± 0.0	(0 – 2)	14.9 ± 2.6	(0 – 89)
	WTD	11.1 ± 0.8	(1 – 26)	7.0 ± 0.9	(0 – 31)
	EDW	347.1 ± 28.6	(24 – 1548)	167.0 ± 23.0	(0 – 1183)
	ERW	0.0 ± 0.1	(-1.5 – 2.3)	-0.01 ± 0.07	(-1.6 – 1.7)
	PXW	5.0 ± 1.2	(0 – 76)	5.4 ± 2.0	(0 – 158)

Table 5.4. Best-approximating models (≤ 8 Quasi-Akaike's Information Criterion [QAIC] of the top ranked model) and the null model from the multi-scale (study site and nesting site) analysis examining pintail duckling survival as a function of duckling age (AGE), brood hatch date (HATD), landscape type (LAND), percent grassland and wetlands within study areas (GRASS, WETL) and nesting habitat type (HAB) from study areas in southern Saskatchewan, 2011 – 2012. Sequential analysis established (A) a biological baseline as the top model structure for duckling age effects then compared variables across scales measured at the (B) landscape (i.e., study site); and (C) nesting habitat scales. The biological null includes an intercept and age effect term. Full model tables are present in Appendix C.

Model Terms	k*	$QAIC_c$†	$\Delta QAIC_c$‡	w_i⁑	-2LL**
A) Biological Null (AGE)					
DSR_{Age}	2	614.51	0.00	0.99	1825.41
$DSR_{1\text{-}7d,\ 8\text{-}30d}$	2	624.08	9.57	0.01	1854.04
DSR_{Week}	2	636.60	22.10	0.00	1891.48
DSR_{Null}	1	736.70	122.19	0.00	2196.74
B) Study Site					
AGE + LAND + HATD	4	607.31	0.00	0.67	1791.92
AGE + GRSS + HATD	4	611.47	4.16	0.08	1804.37
AGE + HATD	3	612.11	4.80	0.06	1812.25
AGE + LAND	3	612.28	4.97	0.05	1812.77
AGE + WETL + HATD	4	612.87	5.56	0.04	1808.55
C) Nesting Habitat					
AGE + HAB + HATD	6	606.12	0.00	0.80	1776.40
AGE + HAB	5	609.84	3.72	0.12	1793.51
AGE + HATD	3	612.11	5.98	0.04	1812.24
AGE + WW + HATD	4	613.83	7.70	0.02	1811.41

* Number of estimable parameters
† Akaike's Information Criterion adjusted for sample size and overdispersion
‡ Difference in QAICc compared to the best-approximating model
⁑ Model weight
** -2 x Log-Likelihood

Table 5.5. Best-approximating models (≤ 8 Quasi-Akaike's Information Criterion [QAIC] of the top ranked model) and the null model from the exploratory analysis examining pintail duckling survival as a function of duckling age (AGE), hatch date (HATD), percent seasonal wetlands (WT3), percent perennial cover (PPC), percent winter wheat (PWW), and edge density of wetlands (EDW) and grasslands (EDG) immediately surrounding the broods, southern Saskatchewan, 2011 – 2012 (YR). Sequential analysis established a biological baseline as the top model structure for duckling age effects then compared variables measured at the brood travel route scale. The biological null includes an intercept and age effect term. Full model tables are present in Appendix C.

Model Terms	k*	$QAIC_c$†	$\Delta QAIC_c$‡	w_i⁑	-2LL**
Brood Route					
AGE + WT3 + PPC + EDW	5	585.79	0.00	0.66	1721.58
AGE + WT3 + EDW	4	589.55	3.77	0.10	1738.83
AGE + HATD + WT3 + EDW	5	590.30	4.51	0.07	1735.08
AGE + WT3 + EDG + EDW	5	590.67	4.88	0.06	1736.19
AGE + WT3 + EDW + YR	5	590.83	5.05	0.05	1736.67
AGE + WT3 + EDW + PWW	5	591.19	5.40	0.04	1737.73

* Number of estimable parameters
† Akaike's Information Criterion adjusted for sample size and overdispersion
‡ Difference in $QAIC_c$ compared to the best-approximating model
⁑ Model weight
** -2 x Log-Likelihood

Table 5.6. Estimated pintail productivity (# of expected nests and ducklings) based on published estimates of nest density, nest survival, average clutch size, average brood size and duckling survival rates for northern pintails in the Prairie Pothole Region. Estimates are scaled to 65 ha (1/4 section) of winter wheat and spring-seeded cropland and landscape-level estimates are scaled based on a landscape composition that consist of 60% spring-seeded cropland and 10% fall-seeded crop.

Habitat Type	Expected Number of Hatched Nests (65 ha)	Expected Number of Hatched Ducklings[⁑] (65 ha)	Expected Number of Fledged Young[**] (65 ha)	Expected Number of Fledged Young[**] (Study Site)
Winter wheat	9.6[*]	66.2	24.7	24.7
	3.8[†]	26.1	9.7	9.7
Spring-seeded	0.2[*]	1.6	0.4	2.2
	1.2[†]	8.5	1.9	11.5
	0.1[‡]	0.7	0.2	0.9

[*] Calculated from habitat specific nest densities and survival rates as reported in Devries et al. (2008)
[†] Calculated from habitat specific hatched nest densities as reported in Skone et al. (2015)
[‡] Calculated from habitat specific nest densities (Devries et al. 2008a) and modeled survival rate for spring-seeded cropland (Devries et al. 2018)
[⁑] Calculated using mean brood size of 6.9 ducklings/per nest as derived from this study
[**] Calculated using cumulative 30-day survival as derived from Figure 2.6 (WW = 37.3%, SS = 22.5 %)

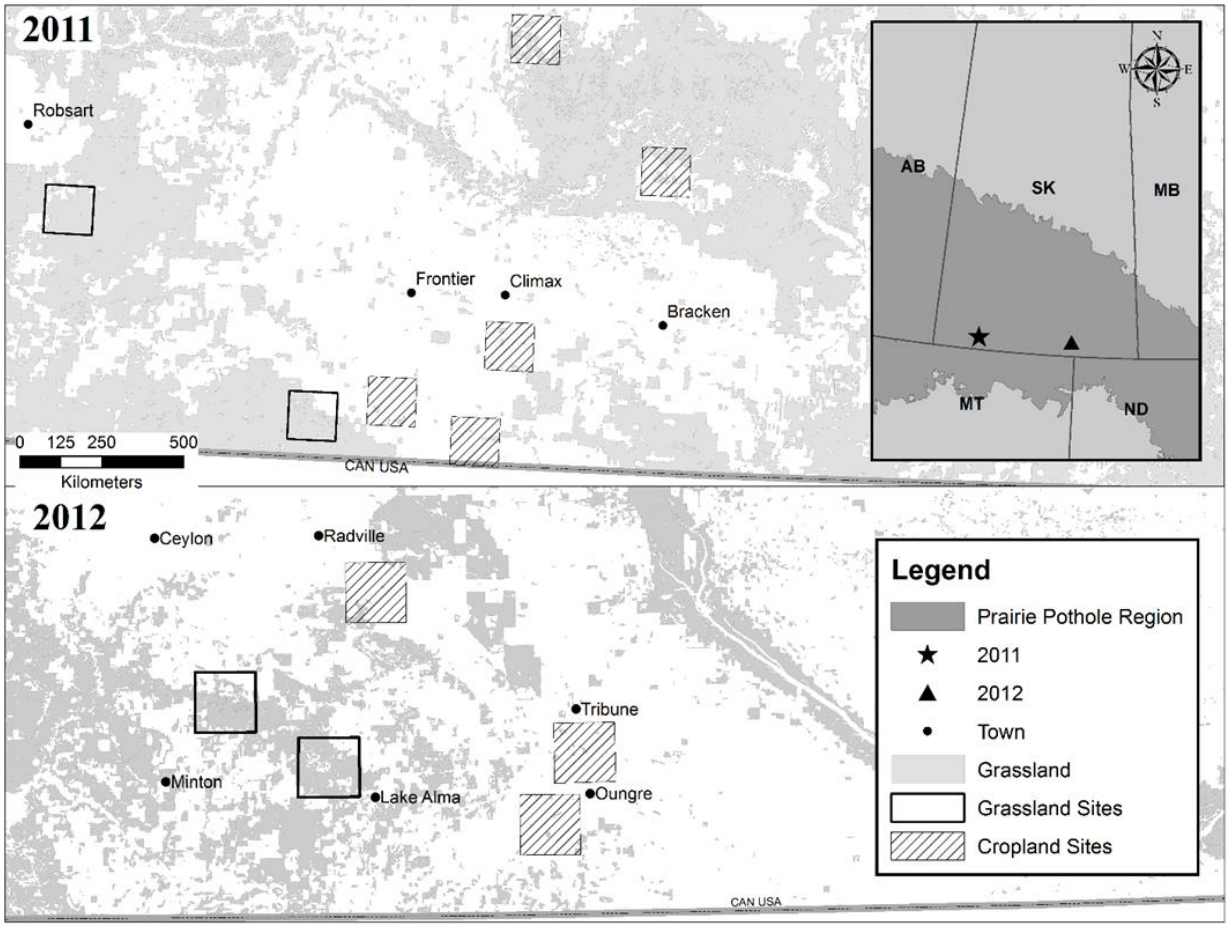

Figure 5.1. Location of study areas and study sites selected to examine duckling survival rates for northern pintails breeding in cropland- and grassland-dominated landscapes within the Prairie Pothole Region of southern Saskatchewan, 2011 – 2012.

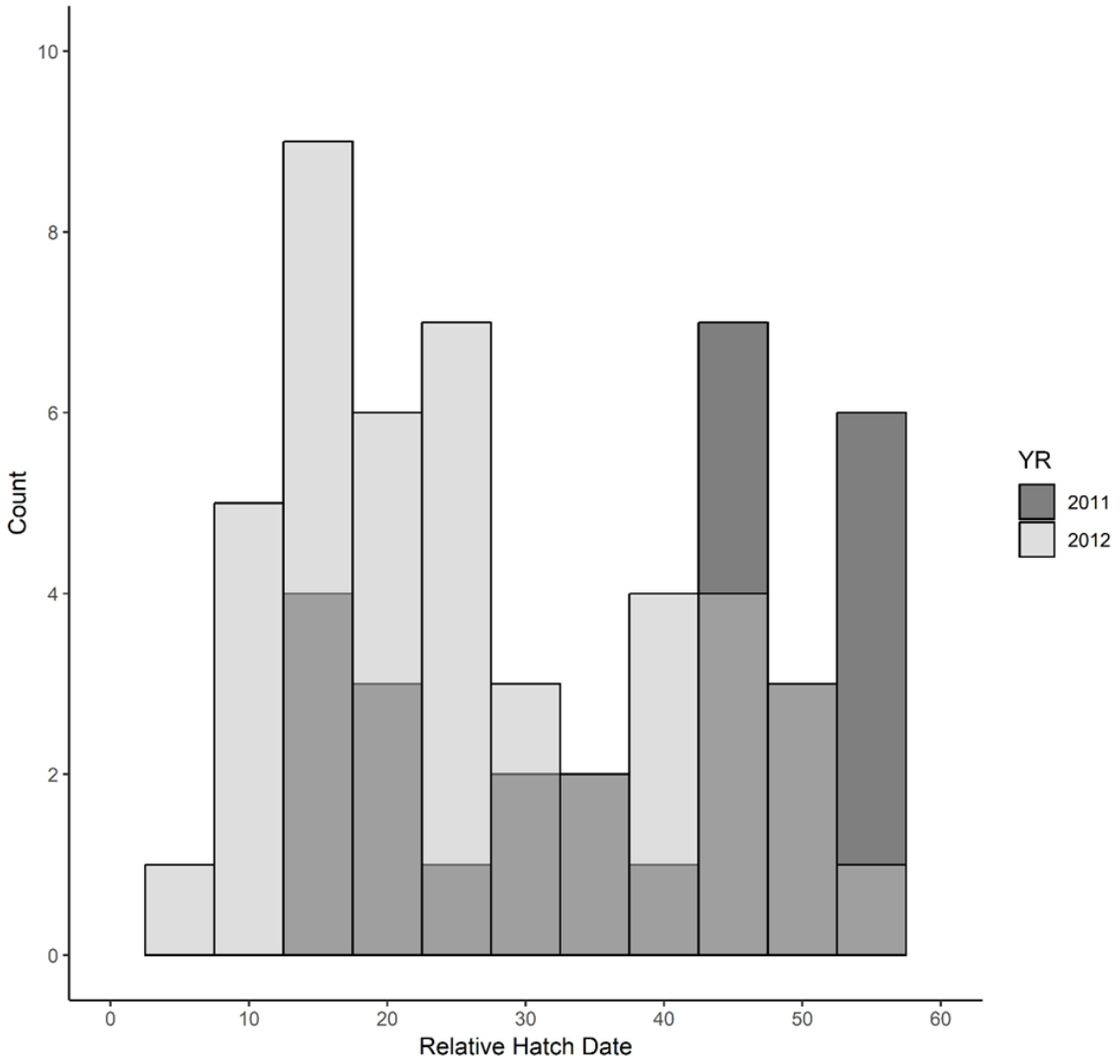

Figure 5.2. Distribution of predicted hatch dates for nests of female northern pintails captured, radio-marked and monitored in southern Saskatchewan, 2011 – 2012. Relative hatch date is based on the first nesting attempt detected from all pintail nests in each year (17 May 2011 and 16 May 2012).

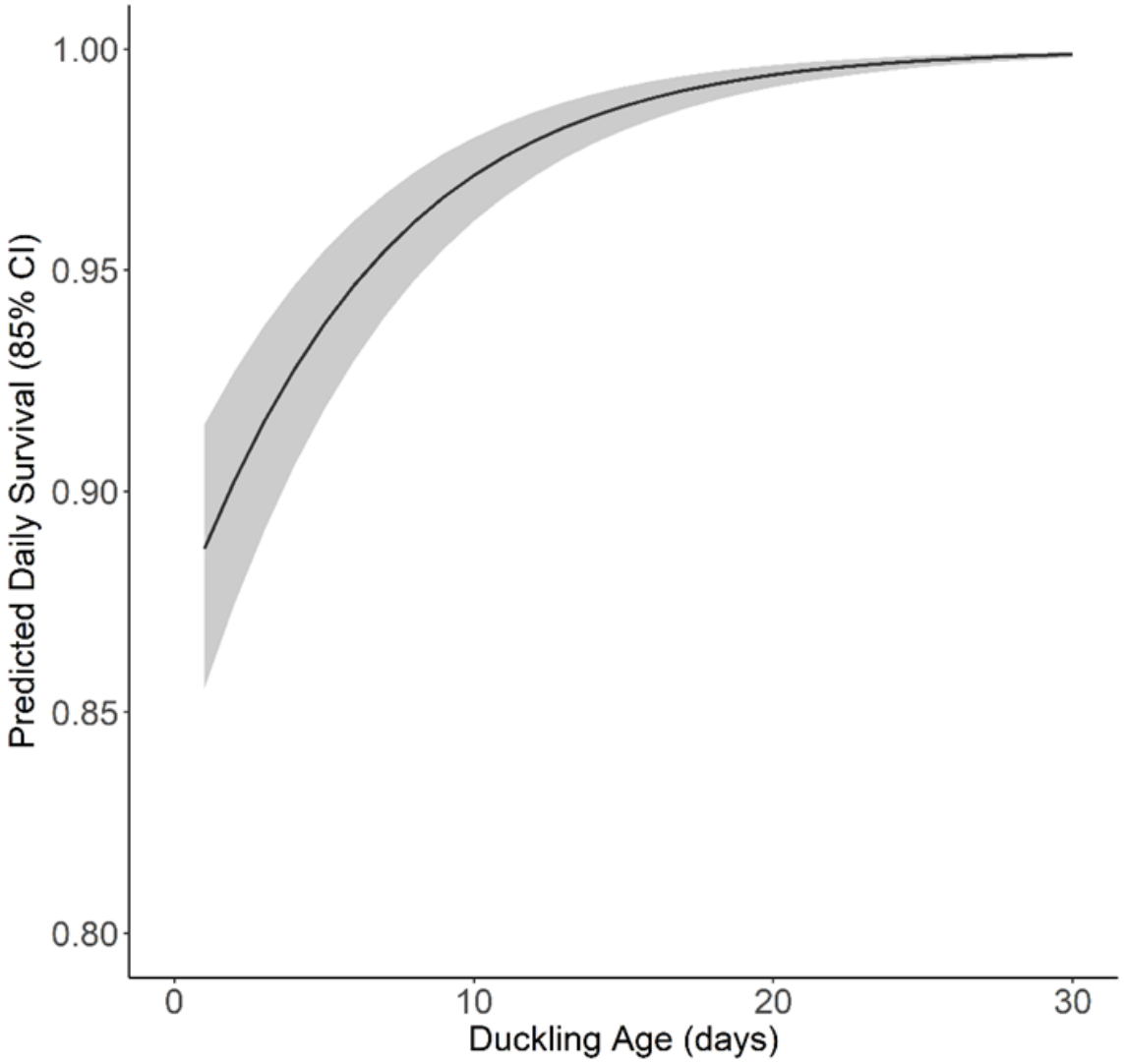

Figure 5.3. Predicted daily survival (%, ± 85 % CI) of northern pintail ducklings (n = 608 ducklings, 88 broods) in southern Saskatchewan, 2011 – 2012. Estimates were derived from the top ranked model in Table 5.2. and included covariates (β ± SE) of duckling age (0.164 ± 0.011), landscape (0.508 ± 0.114), and hatch date (0.013 ± 0.003).

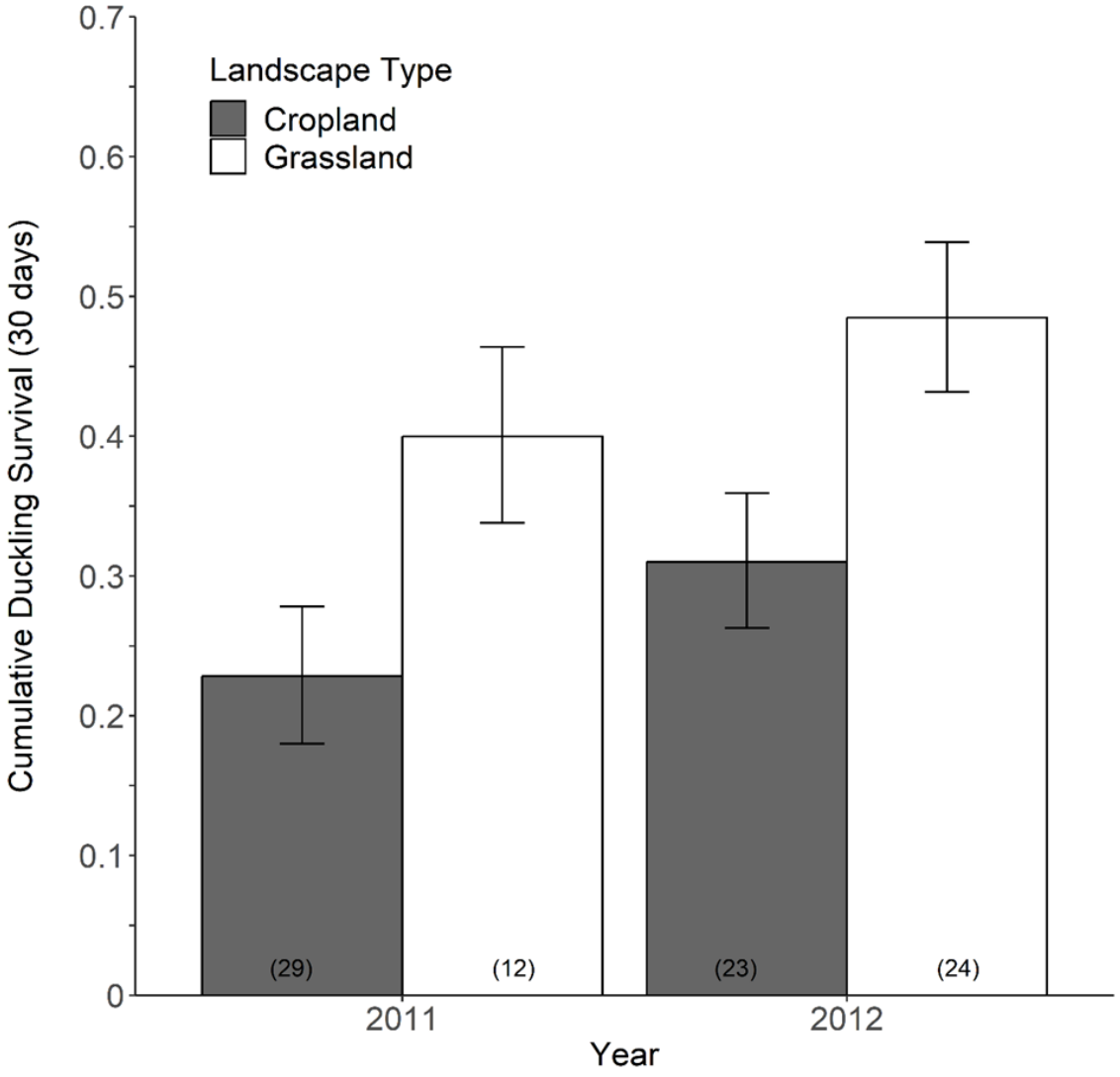

Figure 5.4. Cumulative pintail duckling survival over a 30-day period in relation to dominant landscape type in southern Saskatchewan, 2011 – 2012. Filled bars indicate dominant landscape type at the study site scale and error bars represent 85% confidence intervals. Sample sizes are bracketed.

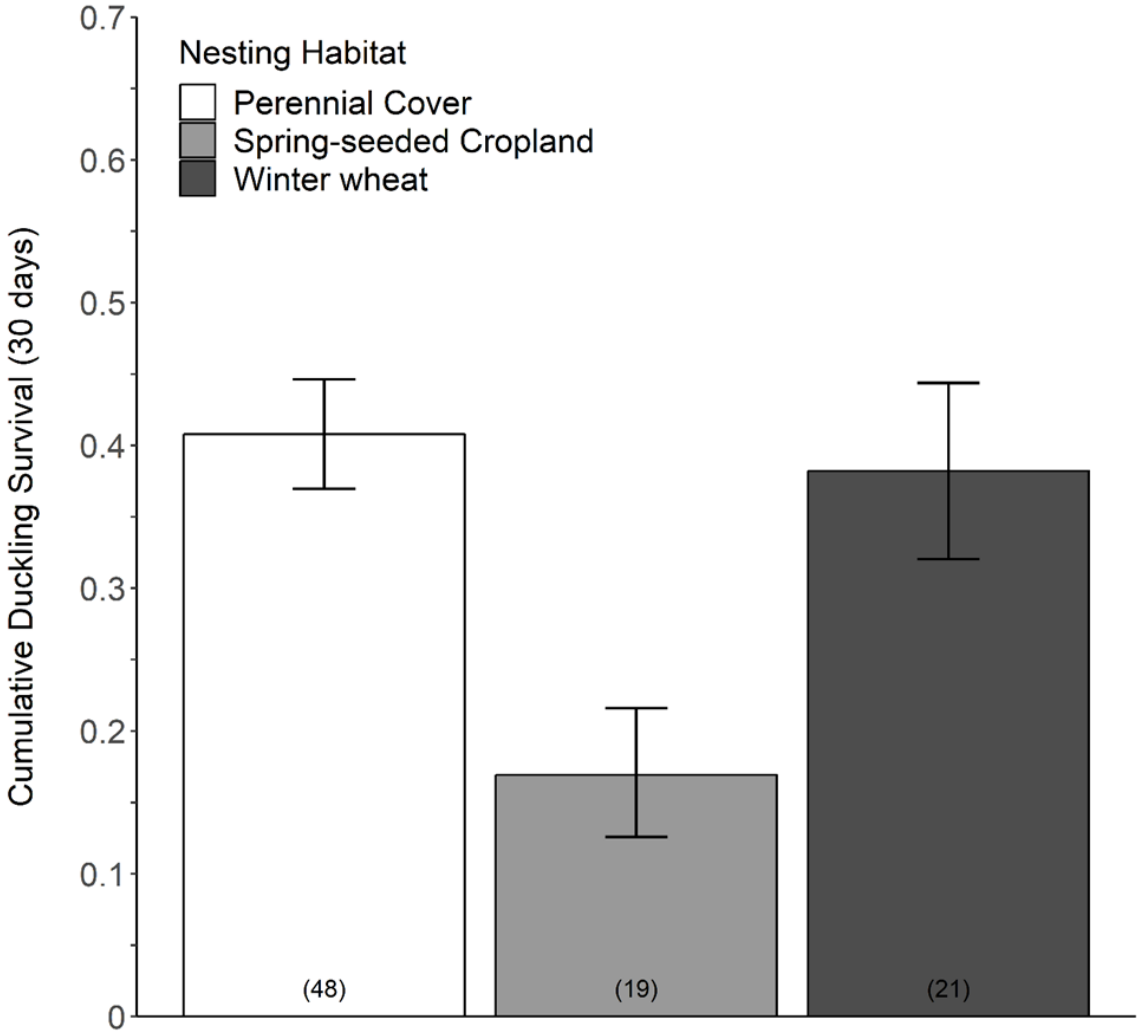

Figure 5.5. Cumulative pintail duckling survival over a 30-day period in southern Saskatchewan in relation to dominate nesting cover type. Filled bars indicate nesting habitat and error bars represent 85% confidence intervals. Sample sizes are bracketed.

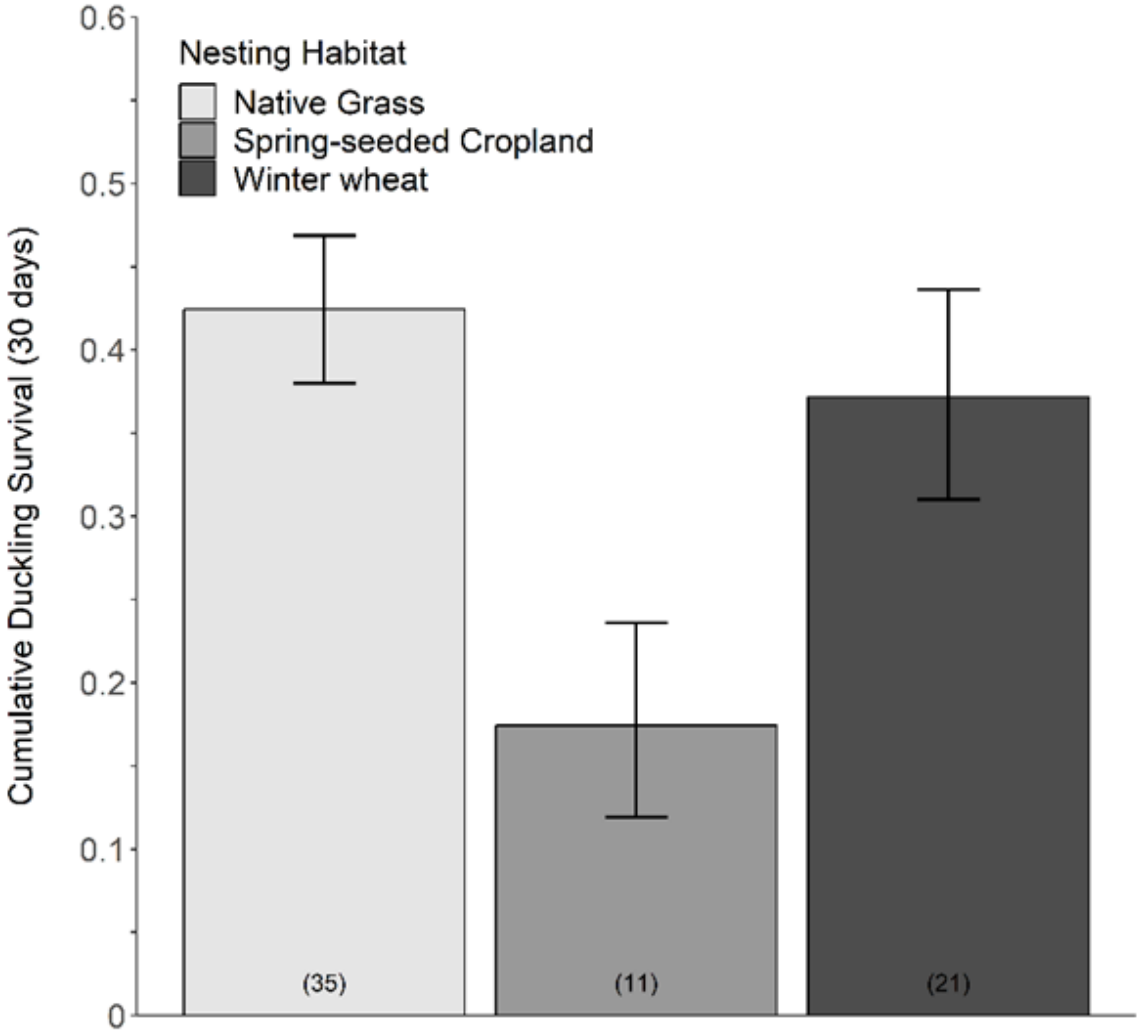

Figure 5.6. Cumulative pintail duckling survival over a 30-day period limited to broods that originated from spring-seeded cropland compared to fall-seeded cropland, southern Saskatchewan, 2011 – 2012. Filled bars indicate nesting habitat type and error bars represent 85% confidence intervals. Sample sizes are bracketed.

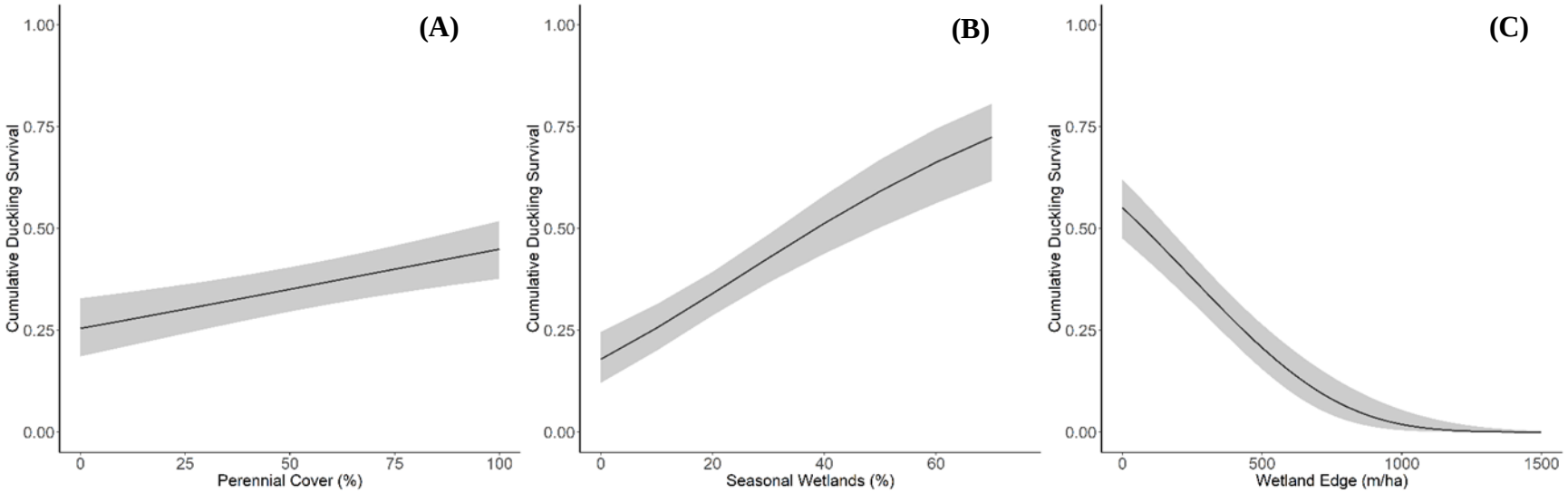

Figure 5.7. Cumulative pintail duckling survival and 95% confidence intervals derived over a 30-day period in relation to upland and wetland cover type and configuration surrounding pintail broods from study sites in southern Saskatchewan, 2011 – 2012. The best-approximating model included age effects, relative proportion of (A) perennial cover, (B) seasonal wetlands, and (C) edge density measured for the wetland – upland interface.

CHAPTER 6. INDIVIDUALS VERSUS ENVIRONMENTS: INTRINSIC AND EXTRINSIC INFLUENCES ON WATERFOWL REPRODUCTIVE SUCCESS

6.1 Introduction

Reproduction is a costly endeavour for many birds and the factors that influence decisions about whether to invest in breeding, how much to invest and when to abandon efforts in favor of future survival are key questions for avian ecologists (Lack 1966, Stearns 1989). The drivers of variation in avian reproductive success can broadly be grouped as restraints by an individual (i.e., breeding decision), constraints within individuals (i.e., intrinsic quality), or constraints imposed from the surrounding environment (i.e., extrinsic or environmental quality). Assuming that individuals respond to environmental changes prior to population-level responses, the simultaneous consideration of both intrinsic individual quality, reproductive investment and environmental constraints enables more detailed understanding of reproductive ecology and the implications of functional responses to changes in habitat quality much earlier than population level demographic change alone (Marra and Holberton 1998, Ellis et al. 2012).

Migratory species such as waterfowl transition between major life cycle phases in distant locations and under variable environmental conditions, where individuals may transition between life cycle stages, seasons or geographic regions in various 'states' or individual quality (Harrison et al. 2011). Additionally, if reductions in individual condition are severe, then effects may persist into subsequent seasons (i.e. carry-over effect; COE) and impinge on future reproduction or survival. Harrison et al. (2011) defined COEs as "events and processes occurring in one season that result in individuals making the transition between seasons in different states (levels of condition), consequently affecting individual performance in a subsequent period". When studying COEs, Harrison et al. (2011) recommended that both intrinsic (individual quality) and extrinsic (environmental quality) factors be considered to properly identify contributing processes.

The simultaneous contribution of both intrinsic and extrinsic factors complicates investigations interested in disentangling relative effects, including reproductive or survival trade-offs, between environments and individuals. Studies of breeding success in waterfowl have examined a variety of factors that influence reproductive outcomes, including maternal age

(Hepp and Kennamer 1993, Blums Hepp and Mednis 1997), body condition (Krapu 1981, Ankney Afton and Alisauskas 1991, Gloutney and Clark 1991, Blums, Mednis and Clark 1997, Devries et al. 2008b), timing of breeding (Raquel et al. 2016), population characteristics (Gunnarsson et al. 2013, Feldman et al. 2016), habitat quality (Clark and Nudds 1991, Horn et al. 2005) and regional effects (Beauchamp et al. 1996, Dunn and Winkler 2010, Sedinger and Alisauskas 2014). Yet, determining the relative effects of each factor provides insights into trade-offs, thresholds and decision points that can limit waterfowl populations.

Intrinsic factors such as indices of individual quality or condition are typically derived from measures of body mass at a single point. Hormones can also act as a measure of condition since they rapidly respond to subtle physiological changes in energetic demands compared to modification of body mass (see Chapter 2). Corticosterone (CORT) is a glucocorticoid hormone secreted by the hypothalamic-pituitary-adrenal axis whose primary purpose is energy regulation (Landys et al. 2006). Hormone activity levels increase in response to changes in energy demands and environmental challenges (Bonier et al. 2009a). An individual's allostatic load is the sum of all energy demands required for daily existence, such as the maintenance of homeostasis and foraging activity (Landys et al. 2006). Energetic demands which increase fitness, such as reproduction, have a positive relationship with CORT (Bonier et al. 2009a) but sustained elevation in CORT can reduce survival or performance (Bonier et al. 2009b). Variation in CORT has also been related to habitat quality, weather, personality, reproductive performance and survival (Marra and Holberton 1998, Angelier et al. 2007, Cockrem 2007, Bonier et al. 2009b).

In birds CORT is incorporated into feather tissue ($CORT_f$) during growth, representing a record of both baseline and acute energetic responses during growth over a period of days to weeks (Bortolotti et al. 2008) and persists with the bird until the feather is moulted. Waterfowl such as mallards (*Anas platyrhynchos*) have an alternate moult strategy with two moults within each cycle (Pyle 2008). A partial pre-alternate moult of body feathers occurs in pre-breeding in late winter and a complete pre-basic moult of wing and body feathers occurs post-breeding in late summer (Pyle 2008). Feathers grown in different seasons and locations incorporate circulating levels of CORT thereby enabling use of $CORT_f$ to index individual quality through cross-seasonal effects. For example, as $CORT_f$ reflects energetic demands during feather growth (see Chapter 2) and provides a spatial and temporal record of CORT (see Chapter 3), then

correlating $CORT_f$ levels to events that occurred prior to and following feather growth provide a unique opportunity to examine the influences of both past and future reproductive performance.

Other intrinsic factors such as maternal age, nest initiation and hatch date influence reproductive investment (Devries et al. 2003, Arnold et al. 2012), yet the effects of female age and body condition on other downstream reproductive stages (i.e., duckling survival) is less clear. Female age does not appear to have a direct effect on duckling survival (Guyn and Clark 1999, Chapter 4); however Blums et al. (2002) found evidence of indirect effects through earlier hatch dates among older females. Relationships between body condition and duckling survival are also complicated as Amundson et al. (2011) did not find direct effects of female body condition on mallard duckling survival; Blums et al. (2002) found that body condition was more influential than age in European ducks and, in Chapter 4, I showed that duckling survival rates were negatively associated with female body size in pintails. Hatch date also influences nest success, duckling and first year survival (Dzus and Clark 1998, Guyn and Clark 1999, Blum et al. 2002, Chapter 4). Analysis of mallard survival rates in the Canadian Prairies reported that adult females which raised broods late into the season had significantly lower subsequent survival compared to females that never hatched a nest (Arnold and Howerter 2012). Considering that female survival during brood rearing is relatively high, Arnold and Howerter (2012) hypothesized that lower survival resulted from limited time to moult and prepare for migration. Therefore, a trade-off may occur between successful reproduction and acquiring enough resources to moult and migrate in optimum condition. If severe enough, then these effects may persist across seasons and reduce future reproduction or survival (Lehikoinen et al. 2006, Leganeux et al. 2013, Sedinger and Alisauskas 2014).

Extrinsic factors such as the surrounding habitat influence components of reproductive success such as survival of nests and ducklings. Individuals in poorer quality habitat may be exposed to higher predation or require increased effort or workload to secure resources for self-maintenance or their offspring. Duckling survival reportedly declines as perennial cover increases (Amundson and Arnold 2011, Bloom et al. 2012), a result that is counter to findings for nest survival (Stephens et al. 2005). However, the relationship between wetland abundance and duckling survival is more consistent across studies, with survival being positively related to seasonal wetland abundance (Pietz et al. 2003, Krapu et al. 2006, Bloom et al. 2012 and see Chapter 5).

I sought to incorporate both extrinsic and intrinsic factors (including physiological hormone biomarkers) together to examine their relative influences on reproductive success for breeding waterfowl and assess potential for a COEs from prior time periods. My objective was to determine the relative importance of intrinsic and extrinsic factors in contributing to reproductive performance (fledging success). Specifically, I aim to determine **1)** if breeding performance or environmental conditions influence subsequent $CORT_f$ levels, and **2)** the relative contributions of past and current intrinsic factors compared to effects of the breeding landscape in influencing avian reproductive success. Using a combination of feather collections, a long-term mark-recapture dataset, and a large-scale intensive study of mallard reproductive success, I evaluated how antecedent factors influence reproductive success and if long-lasting impacts on future reproduction exist, while simultaneously assessing contributing factors to individual reproductive performance.

6.2 St. Denis Recapture Study

6.2.1 Study Site and Field Methods

To assess potential factors that influence feather corticosterone, I used mallard reproductive data collected during 1983 – 2000 from a long-term study at St. Denis National Wildlife Research Area (52° 12'N, 106° 5'W), located approximately 40 km east of Saskatoon, Saskatchewan. The 361 ha study area is characterized by undulating agricultural landscape with abundant temporary, seasonal, semi-permanent and permanent wetlands (Stewart and Kantrud 1971), which are fringed by shrubs, trees and perennial grasses. The surrounding area is dominated by agricultural land-use consisting of spring cereal crop production as well as cattle pasture and forage crops. More detailed description of the study site can be found in Clark and Shutler (1999).

Nest searches were conducted from early May to mid-July, by flushing nesting females using rope or chain drags and on-foot searches (Clark and Shutler 1999). Then, nests were monitored every 7 to 14 days to determine clutch size, clutch initiation date and nest fate (i.e., hatched, destroyed, abandoned). If successful, then initial brood size was estimated and broods counted weekly until total brood loss, abandonment (i.e., brood failure), or ducklings reached 30 days in age (i.e., fledged). As per the broader dataset, females suspected of losing a brood were observed multiple times to confirm total brood loss and we assumed total loss if females

abandoned a brood prior to 30 days in age. Female mallards were trapped on the nest during late incubation and marked with a unique leg band and nasal marker combination (Arnold and Clark 1996, Dufour and Clark 2002). Body mass, length of wing and head were recorded, and a greater secondary covert feather was collected for age assignment and feather corticosterone analysis. All capture and marking protocols were reviewed and approved by the University of Saskatchewan's Animal Care Committee on behalf of the Canadian Council on Animal Care

6.2.2 Environmental Covariates

Environmental data for St. Denis were obtained from Environment Canada's weather monitoring station located at the Saskatoon Airport (52° 10'N, 106° 43'W) to index temperature at St Denis (Drever and Clark 2006). Mean daily temperature for both July and August were calculated for each year as well as mean minimum and maximum temperatures. I calculated monthly precipitation totals for July and August from daily accumulation records; however, Drever and Clark (2006) found that monthly precipitation at SDNWA was only moderately correlated with equivalent amounts in Saskatoon. Therefore, to provide an estimate of the relative wetland conditions in each year I also considered two competing indices; pond depth and pond count. Pond depth was recorded in spring from a reference pond and pond counts were calculated based on wetland numeration conducted in early May of each year.

6.2.3 Feather Corticosterone

Feather corticosterone processing, assays and protocols were identical to those stated in previous chapters, where the mean inter- and intra-assay CV was 10.1% and 9·4 %, respectively (n = 4). I selected recapture records from birds which had feathers collected in the year following a monitored breeding attempt (i.e., females bred and were monitored in two consecutive years). I assume that birds breeding in St. Denis stayed to moult wing feathers in the region. However, post-breeding mallards can make short distance migrations to moult and grow wing feathers. The environmental metrics I used may only partially reflect conditions experienced during wing feather growth. I excluded all females with unknown nest fate, or when nests were abandoned or destroyed due to investigator disturbance (n = 4). I estimated female pre-laying body condition during breeding using a scaled mass index (SMI) relative to predicted bird mass given wing length as an indicator of structural size (Peig and Green 2009). Three females had missing body

morphometric data, so I calculated the structural mass index correction excluding these individuals, then replaced with the mean morphometric value to generate a SMI score.

6.2.4 Data Analysis

Each record consisted of data from two time periods for each female: time *t* included a capture and monitored breeding attempt plus a recapture and feather collection in time *t+1*. Ten birds were recaptured in multiple years, so I tested for correlations between body mass and $CORT_f$ between time *t* and *t+1* and used linear mixed effect models to determine if variation in $CORT_f$ was related to environmental or reproductive indices. I included bird identity as a random effect to account for multiple samples from the same female (i.e., across years). Random effects did not explain additional variation or improve model fit so I used linear regression for all subsequent analyses using a log-transformed response to improve normality. All models included clutch initiation date to account for the effects on body condition and clutch size within a season). I attempted to avoid pseudo-replication by including only single year-level covariates in each model (i.e., temperature, wetland condition; Legagneux et al. 2013). I compared models using information theoretic procedures (Burnham and Anderson 2002), where models with a lower Akaike's Information Criterion (AIC) are favored unless the difference in AICc (ΔAICc) was ≥ 2. I used restricted maximum likelihood for parameter estimation of top-ranking models.

6.3 Mallard Assessment Study

6.3.1 Study Site

During 1993 – 2000, female mallards were captured and monitored for the duration of the breeding season to investigate influences of intrinsic and extrinsic factors on reproductive investment and success (Howerter et al. 2014). Nineteen study sites (each approx. 65 km^2) were in the Aspen-Parkland, Mixed Grassland and Boreal Transition ecoregions of Alberta, Saskatchewan and Manitoba (Figure 6.1). Land use on each study site was primarily annual cereal and oilseed crop production, with varying amounts of pasture (native and tame grasses) and forages for beef cattle. Areas not in agricultural production included numerous temporary, seasonal, semi-permanent and permanent wetlands (Stewart and Kantrud 1971); along road and railway rights-of-way; fence lines, and remnant patches of trees, shrubs and grasses (Table D.1). One to three sites were monitored in a single year and each site was studied for one breeding season. More detailed site selection and descriptions are provided in Howerter et al. (2014).

Female mallards were captured between 4 April to 5 May, a period corresponding to pair arrival and prior to the first recorded nesting attempt using decoy traps (Sharp and Lokemoen 1987). Trapping lasted approximately two weeks, where chronological differences in trapping dates reflected variation in site-specific mallard arrival dates (Figure 6.2). Birds were banded with a metal leg band and body morphometric measurements taken: arrival body mass using a 1.5 kg Pesola hand-held scale (nearest 10 g); wing length (nearest 1mm) using a flat board ruler from the end of the carpo-metacarpus to the tip of the longest primary feather; and head length from the back of the head to the tip of the bill using dial calipers (nearest 0.1 mm). Pre-laying body condition was estimated using a scaled mass index (SMI) relative to predicted bird mass given wing length as an indicator of structural size (Peig and Green 2009). A greater secondary covert (GSC) feather was collected to classify female age as second-year (SY; i.e., yearling) or after-second-year (ASY; i.e., adult) based on feather characteristics in comparison to a collection of feathers from known-age individuals or assigned using discriminant function analysis (Krapu et al. 1979). Birds were radio-tagged using IMP/150 22g intra-abdominal radio-transmitters (Telonics, Mesa, AZ; Rotella et al. 1993). All capture and handling protocols were reviewed and approved by the University of Saskatchewan's Animal Care Committee on behalf of the Canadian Council on Animal Care.

6.3.2 Reproductive Investment and Success Variables

Information from radio-marked females was used to measure individual quality, reproductive timing, investment and success. Females were monitored using vehicle-mounted null-array antenna systems and triangulation (Kenward 2000) starting one day post-marking until either death, radio failure, departure from the study area, brood fledging, or membership in a non-breeding flock. Searches for missing females were conducted within and outside study boundaries using available roads and weekly flights with fixed wing aircraft. Females were located twice daily between 0600 and 1300 h; a period with high probability of female nest attendance (Gloutney et al. 1993).

When females were located at the same location for three consecutive tracking periods, the suspected nest location was visited on foot, flushing the female to locate the nest (1993 and 1994) or identified using handheld telemetry and triangulation (1995 – 2000). Investigators then returned to find the suspected nests in the afternoon, when females are typically absent. Nests were defined as having ≥ 1 egg present at the female's location. Clutch initiation date (CID) was

estimated for nests found during laying by back calculating nest age, assuming one egg laid per day or for nests found during incubation by estimated incubation stage (Weller 1956), and clutch size. All initiation dates were then scaled at each site relative to date of the first recorded nest (i.e., start of the nesting season). Nests were visited once prior to hatch to determine minimum clutch size.

To determine fate, nests were visited when females were absent from the nest location for two consecutive tracking periods and classified as active, abandoned, hatched, or destroyed. A nest was considered successful if ≥ 1 egg hatched (Klett et al. 1986). Based on a season-long tracking history, I calculated the total number of nests per female (NST) and eggs laid (EGG). Then I derived a measure of total nesting investment (NINV) as the seasonal sum of days spent laying and incubating until hatch or loss of nest. Clutch initiation date (CID) was determined using predicted initiation date based on incubation stage during nest visits and tracking histories. Brood size at hatch (YNG) was based on the difference between clutch size at the last visit and the number of unhatched eggs remaining in the nest (Orthmeyer and Ball 1990). Brood-rearing females were tracked once daily and ducklings were counted weekly using passive observation until either total brood loss, abandonment (i.e., brood failure), or fledging. Brood loss was assumed if females abandoned broods prior to 30 days in age and were visited multiple times to confirm loss. However, this assumption may underestimate brood success if abandoned ducklings are adopted and otherwise survive (see Clark et al. 2005). Ducklings were considered fledged at 30 days in age (see Chapter 5) with the number of fledged young per brood summed (FLG).

6.2.3 Environmental Variables

To account for the influence of site-specific habitat on reproductive success, I summarized the relative amounts of grassland, perennial cover (grassland, hayland, and planted cover), annual cropland and wetlands at each study site using ArcGIS (see Table D.1). Habitat classification was based on infrared aerial photographs taken in July of the year of study and wetland basin visits between late June and early August. To provide an estimate of the relative wetness of each site, I assessed two competing indices: relative pond index and Palmer Drought Severity Index. The pond index (PND) compares the relative wetness of a site to its long-term (1970-2000) average as determined from the United States Fish and Wildlife Service Waterfowl Breeding Pair and Habitat Survey pond counts (Benning 1976). Year-specific standardized

deviations in median pond counts at the survey segment level were interpolated using standardized inverse distance weighting. The Palmer Drought Severity Index (PDSI) is an index of meteorological drought conditions across North America, using temperature and precipitation data to quantify relative aridity long-term changes in drought and surface water balance (Dai et al. 2004). I also used the average pond density within the site. These three indices were compared against each other to determine which explained more variation in the reproductive data and pond index was selected as the best measurement of current wetness.

6.2.4 Feather Corticosterone

I measured levels of $CORT_f$ from collected wing feathers following procedures established by Bortolotti et al. (2008) and outlined in previous Chapters. $CORT_f$ extraction efficiency was assessed as recovering > 97 % of the radioactivity within reconstituted samples with feather samples randomized, run blind and measured in duplicate. Assay variability was assessed using the coefficient of variation (CV) of known standards run in duplicate across all assays, with a limit of 15% CV (± SD) as per previously published $CORT_f$ literature (Bortolotti et al. 2008, Fairhurst et al 2012). For the larger mallard dataset, the average intra-assay variation was 8.95 % (range 3.6% to 14.1%) and inter-assay variation was 8.2%. All samples were above detection limits (ED80) of 18.3 pg 100 μl^{-1}. Serial dilutions of mallard feather samples revealed displacement curves that were parallel to standard curves. As feathers are believed to grow in a time-dependent rather than mass-dependent manner, I expressed [$CORT_f$] in pg mm^{-1} (Bortolotti et al. 2008, Bortolotti 2010, Romero and Fairhurst 2016) with all $CORT_f$ analyses performed at the Department of Biology, University of Saskatchewan, Canada.

6.2.5 Data Analysis

This study uses reproductive and site level data from a subset of study sites within the Prairie-Parklands. To examine whether landscape factors influence reproductive success I selected sites which represent strong differences in areas of perennial cover and wetlands (Howerter et al. 2014). Study site were ranked using Principal Components Analysis (PCA) of habitat and wetland variables, including: the amount of each upland habitat type (composition), wetlands (composition, density and abundance) and wetness score (PDSI, PND). The first three principal components explained >88% of the variation, with PC1 representing a cropland (loading = 0.471) and perennial cover (loading = -0.485) gradient, PC2 reflected wetland

abundance (wetland density = 0.596, Count = 0.536) and PC3 reflected longer term drought conditions (PDSI = 0.872). Sites were then ranked and selected to represent variation across these three gradients (grasslands-cropland, many-few basins and wet-dry conditions).

I used a staged approach to randomly select a subset of female mallards for $CORT_f$ analysis. I first restricted sampling to females captured prior to 5 May (pre-laying period), assigned an age category with high certainty, remained on the study site with a continuous daily tracking history for the entire breeding season (i.e., until there was no evidence of breeding activity or the female was killed/departed permanently). In addition, I retained females with high likelihood that reproductive fates for each stage (nest, female and brood) were known. Then, I created a reproductive investment index to assign birds to one of three reproductive scenarios: (1) females with no detected nests (i.e., presumed non-breeders), (2) birds that nested but did not hatch a brood (i.e., failed nesters), and (3) birds that nested and hatched a brood (i.e., successful nesters). Females were randomly selected from all birds in each category captured at selected study sites. I examined parameters for outliers and truncated extreme values (e.g., maximum number of nests = 4; eggs = 21, nesting days = 65, young = 12, and fledged young = 12). I then tested for correlations between model covariates and found relationships between intrinsic parameters with age and year (i.e., $CORT_f$, body mass, and body condition) so I mean-centered $CORT_f$ and body mass values by female age. Extrinsic site-level variables are included as percentages of the study area to aid comparisons between areas.

I used piecewise structural equation model to examine the relative effects of both past and current intrinsic and extrinsic conditions on future reproductive investment and success (Lefcheck 2016). Structural equation models allow for specification and comparison of both direct and indirect relationships to inform assessment of hypothesized causal relationships (Shipley 2009). Classical SEM uses global estimation to assess the goodness-of-fit of covariances between variables, which are displayed using network analysis and path diagrams. In contrast, piecewise SEM uses local estimation to separate the overall path diagram into component linear equations to be evaluated independently which enables incorporation of alternative distributions, sampling designs and random effects. First, I derived two conceptual models which incorporated the variables of interest for **(1)** all birds (e.g., non-breeders, failed- and successful nesters and **(2)** only birds that attempted breeding. Hypothesized paths were included based on previous literature (Figure 6.2). I also included the hypothesized relationships

with $CORT_f$ and other intrinsic variables to test for effects of past physiologic conditions (i.e., energetic demand during wing feather moult from previous summer). Body mass, feather corticosterone, nesting investment and environmental variables were coded as continuous while counts of nests, eggs, and young were coded as ordinal variables.

I separately fit either linear regression models with Gaussian distribution and an identity link function for nests, clutch initiation date and female mass (i.e., normally distributed data) or a generalized linear Poisson model with log link function for egg counts. The numbers of hatched and fledged young depend on breeding decision, and high failure rates for nests and broods result in zero-inflated data for counts of ducklings (hatched and fledged) and nesting investment. Following Cunningham et al. (2018), I used hurdle models within the SEM to separate the two processes with failure (i.e., count of 0) modelled with a binomial distribution and log link function, and success (counts > 1) using either Poisson distribution and log link (hatched and fledged young) or negative binomial (nesting investment). Model residuals were examined to ensure assumptions were met. I tested for support for random effects of year within individual models but did not find adequate support and excluded the term from further consideration. Overall model fit was assessed using directional separation (d-sep) tests (Shipley 2009) to identify important missing relationships, measure model fit (Fisher's C) and aid comparison (Akaike's Information Criterion; AIC). After significant missing paths were included, I then removed non-significant variables if $\Delta AIC < 2$. I calculated standardized path coefficients using the 'relevant range method' (Shipley 2010) which varies the predictor between maximum and minimum values while holding all other predictors at their mean and predicting the change in response as a proportion of its range. Both significant ($P < 0.05$) and near significant ($P < 0.10$; i.e., trend) coefficients and paths are presented. The piecewiseSEM package (Lefcheck 2016) for program R (R Core Team 2015) was used for fitting d-sep tests.

6.4 Results

6.4.1 Influences on Feather Corticosterone (St. Denis)

In total, 42 individuals were recaptured across 9 years. For individuals captured more than once, feather corticosterone was not correlated between capture events (Pearson's r = -0.21). When examining factors which explained variation within $CORT_f$, neither the age of female ($F_{1,42} = 1.061$; $P = 0.31$) nor year of growth ($F_{7,36} = 0.691$; $P = 0.68$) were significant (Figure

6.3). Variation in $CORT_f$ was unrelated to intrinsic female traits (body condition, structural size) and breeding effort (clutch size, brood size or length of brood rearing). Environmental conditions (summer air temperature, precipitation, wetland abundance or water conditions) did not explain any additional variation in $CORT_f$. All tested models were equivalent to a null model. Similarly, female body condition did not differ between ages (P = 0.95) or years (P = 0.97). Levels of $CORT_f$ produced during wing moult in year *t* did not influence body condition measured the following year (*t +1*).

6.4.2 Influences on Reproductive Success (Assessment)

In total, 523 female mallards were used in the analysis, 1993 – 2000. The sample included non-breeders (*n* = 89), failed nesters (*n* = 272) and brood-rearing females (*n* = 162), which provided seasonal reproductive investment scores (NINV) ranging from 0 (i.e., non-breeders). For example, the score of 79 represents a female that tended 3 active nests, laid a minimum of 21 eggs and which produced one brood of 9 that was reared for 6 days.

The path analysis involving all radio-marked females provided insights into factors influencing the "decision" to breed and subsequent fledging success (Figure 6.4). Neither site-specific percentage of grassland nor female-specific $CORT_f$ were retained in this analysis. Wetland variables had positive and negative, sometimes opposing, relationships with reproductive investment and success. Sites with above-average pond abundances attracted females with higher body mass, greater nesting propensity and reproductive investment. Females settling on sites with relatively more area of wetlands were also more likely to breed and made larger investments in nesting but produced fewer fledged ducklings. Intrinsic female traits had opposing influences on nest investment and reproductive success. Older females appeared to invest more in nesting whereas heavier females were likely to breed but had lower nesting success and, possibly, less chance of fledging ducklings.

The path analysis incorporating females that nested at least once confirmed several general relationships reported above and unveiled new ones (Figure 6.5). Females nesting on sites with above-average pond abundances were heavier and experienced greater nest success. Heavier females also nested earlier and more often. Older females and birds nesting on sites with more grassland area produced more eggs. Five variables had direct effects on fledging success (Figure 6.5). Females nesting on sites with more wetland area fledged fewer ducklings, yet this

was partly offset by higher nesting success on these sites. As expected, larger broods produced more fledglings. Direct effects were detected between fledging success associated with clutch initiation date, number of nests and number of eggs, however indirect effects result in trade-offs between timing, investment and success. Late-nesting (re-nesting) females were more likely to fledge duckling(s) and although late nests were more likely to hatch, brood size was smaller relative to early nests. As predicted, females which nested late in the year were likely re-nesting. Although females with more nest attempts did fledge more ducklings, hatching success was lower and brood sizes at hatch were smaller. Females that laid more eggs in a season indirectly fledged more offspring (i.e., through greater hatching success and brood size at hatch) and yet the negative direct path between egg production and fledging success implies a cost associated with investment. Lastly, this analysis revealed possible COEs between past energetic profiles and current reproduction (Figure 6.5). Females with higher $CORT_f$ values tended to make fewer nesting attempts and were less likely to nest successfully.

6.5 Discussion

6.5.1 Influences on Feather Corticosterone (St. Denis)

This study used a long-term mark-recapture study of breeding waterfowl to examine whether patterns in reproductive investment and local environmental conditions were correlated with variation in hormone levels sequestered in feathers. While $CORT_f$ differed among individuals, I did not find any evidence that the intrinsic and environmental variables explained any variation in $CORT_f$. This result suggests that either the lack in response was due to $CORT_f$ not being influenced by these variables or the variables selected were inappropriate for identifying such patterns. A growing body of literature provides evidence of $CORT_f$ responses to energetic demands (Chapter 2, Fairhurst et al. 2011, López-Jiménez et al. 2016, Romero and Fairhurst 2016) however, mechanisms in nature are not fully known. The results from the St. Denis dataset match those found in arctic-breeding common eiders (*Somateria mollissima*) which show low repeatability of $CORT_f$ between years and no evidence to support that body condition or reproductive investment influenced hormone levels in feathers (Legagneux et al. 2013). Similarly, $CORT_f$ was not related to prior breeding experience or reproductive output of tree swallows (Harris et al. 2017). These studies suggest that $CORT_f$ responds to energetic demands, which are not consistent between years or time periods. The physiologic response of a

bird can and does rapidly shift between laying, brood rearing and moulting, the latter two, which may be separate or concurrent. If such energetic demands are not such that they alter body mass gains or reproductive output, then the scale of variation in $CORT_f$ may not align with individual body condition or reproductive effort.

6.5.2 Influences on Reproductive Success (PHJV Assessment)

This study used one of North America's largest datasets of mallard reproductive success to simultaneously examine contributions of extrinsic environmental conditions and intrinsic female traits relative to reproductive investment and success. The top performing model that incorporated breeding status for all birds (Figure 6.4) was well supported by the data but did not explain much variation in nesting investment (i.e., re-nesting) or female mass which suggests other variables may be missing. Female age did not appear to play a large role in the decision to breed, while female mass was negatively associated with hatching success and suggests that smaller females may invest less in nesting and are more likely to experience nest failure. This result matches that of Arnold et al. (2010) who used a larger dataset of nesting mallards and found that re-nesting was lower for smaller females. Mack and Clark (2006) also found females which that did not breed were smaller. The number of fledged young was primarily associated with brood size at hatch, where larger broods would have greater likelihoods of fledging more offspring; however, there were negative direct effects of female mass on both brood size at hatch and possibly the number of fledged young. However, in this path analysis timing of breeding was not a factor which has been shown previously to influence re-nesting propensity, clutch sizes and brood size at hatch (Toft et al. 1984, Elmberg et al. 2005, Arnold et al. 2010).

Site wetness, number of wetlands and female mass were important for influencing the decision to breed but only pond index and wetland abundance influenced how much investment would occur during breeding. For migratory birds, the condition of the individual and its breeding grounds can influence the timing of breeding as internal resources must be balanced between long distance travel, defending territories and nest initiation. For arctic nesting birds, food availability and body condition play must meet thresholds for breeding (Ankney and MacInnes 1978, Chastel et al. 1995); however, mallards are not limited to a single breeding attempt and can initially utilize lipid reserves to meet energy requirements but also obtain resources from the local environment, particularly for re-nests (Krapu 1981). As birds in greater body condition were found in areas with greater wetland abundance and the amount and

abundance of wetlands positively influenced breeding decisions and investment in both first and subsequent nests, these results suggest that local conditions were influential in determining whether a female would breed and how many times. This relationship was highlighted by the direct effect of pond abundance and wetland area on the decision and scale of nesting investment but not directly on reproductive success. Counter to predictions, the composition of grassland did not appear to be an important factor in determining breeding success for mallards, despite evidence suggesting that the amount of grassland influences survival for nests and ducklings in prairie-nesting waterfowl (Stevens et al. 2005, Howerter et al. 2014, see Chapter 5). This result suggests that wetlands play a larger role compared to upland habitats. Similarly, $CORT_f$ was not important for determining whether or when mallards-initiated breeding.

While multiple individual pathways are evaluated in the literature, this study highlights trade-offs between investment and success. For breeding birds, I found that intrinsic traits like female mass had direct effects on timing of breeding as predicted but also directly influenced the number of nesting attempts in a season. This result is consistent with previous studies which reported positive relationships between female condition and re-nesting; however, unlike Arnold, et al. (2010), I did not find that female age was influential. The timing of first breeding displayed a direct path with hatching success; a pathway not hypothesized in the original model. Earlier hatching had a positive effect on overall success where early nests had greater success but smaller brood sizes. Trade-offs between repeated efforts and investment led to reduced returns for fledging success. Although repeated nesting efforts elevated probabilities of successfully hatching young, the consequences of sustained efforts diminished returns likely through time constraints placed on fledging young late in the season and trade-offs with reduced recruitment for late hatched young (Dzus and Clark 1998, Dawson and Clark 2000). Similarly, the number of nesting attempts also showed trade-offs with reproductive success where re-nesting attempts had lower hatching success and smaller broods than just explained by seasonal clutch size reductions. The direct effects to fledging success may reflect the consequences of brood-rearing, where larger broods placed greater energy demands on tending females. Birds which also raise ducklings later in the season, may also have greater commitment to ensuring fledging.

Extrinsic factors of wetland abundance and condition had positive effects on overall hatching success but were not important in determining the degree of success. Although landscapes that had many wetlands or were wetter than long-term averages, had more nests hatch

than drier landscapes, these environments ultimately fledged fewer ducklings. The trade-off between higher wetland abundance and reduced number of fledging ducklings was counter to predictions. Similar to Mack and Clark (2006), I found that nest success was higher for females nesting in areas of greater wetland abundance at the landscape scale but my results differed from other studies of duckling survival (Amundson and Arnold 2011, Bloom et al. 2011, Howerter et al. 2014, see Chapter 5) which have found positive relationships between duckling survival and wetland abundance. Wetlands are attractive foraging habitat for predators which may expose ducklings to higher mortality (Phillips et al. 2003) and the spatial arrangement of wetlands or vegetation configuration that may be important for duckling survival (Bloom et al. 2011, Chapter 5) were not accounted for in my model. I did not find any evidence that grassland composition influenced reproductive success beyond a weak relationship with clutch size. Overall, my results highlight how landscapes apply different pressures on various reproductive components and how landscapes which confer survival benefits to nests are not the same as those for brood-rearing.

Counter to predictions I found weak support that, among nesting birds, those with higher $CORT_f$ had lower re-nesting propensity and hatching success. The lack of evidence for $CORT_f$ to predict breeding decisions nor strong pathways connecting $CORT_f$ to reproductive success suggests that energetic demands from the previous summer did not have a major impact on waterfowl reproductive performance and the current state of the individual (i.e., body mass) was more influential than carry-over effects from the previous summer. Results from the St. Denis dataset and its multiple recaptures did not find any support for prediction of $CORT_f$ using landscape levels variables or reproductive output. As $CORT_f$ responds to energetic demands during periods approximately 6 – 8 months prior, there is ample opportunity for short term response through increased foraging or rest to recover the resources necessary to moult feathers and breed in the following year. Increased energy demands and elevations may occur during breeding but if these effects are not long-term and occur during moult then the $CORT_f$ signatures may not index earlier conditions. Studies which have identified $CORT_f$ signature and carry-over effects have largely occurs in arctic breeding species (Crossin et al. 2013, Legagneux et al.2013, Harms et al. 2015) which rely heavily on acquiring resources during short windows and often are capital breeders (i.e., utilize internal resources obtain prior breeding). Mallards are not strict capital breeders and will acquire resources during migration and on the breeding grounds. I did find variation in feather corticosterone across individuals, which may suggest that $CORT_f$

responds to more localized effects. Future experiments to understand what activities or conditions drive $CORT_f$ signatures in wild populations or manipulations of $CORT_f$ and subsequent monitoring on breeding performance would provide valuable information and are suggested.

Several factors may have played a role as to why several predicted pathways were not supported. Additional factors have been shown to influence reproductive success, including stochastic events, food availability, disease, as well as past experiences and local knowledge. Female age may not be an accurate reflection of experience, which has been shown to be important to reproductive success (Hepp and Kennamer 1993, Blums et al. 1997). Birds may utilize past breeding experiences to optimize breeding success and select habitats which confer greater fitness benefits or higher survival rates during nesting. Additionally, local knowledge may also facilitate experiences of birds. My sampling strategy failed to fully represent the entire natural range of variation in captured individuals. Only birds which arrived on site and were territorial were exposed to capture. Birds which arrived in poor condition or health may not make the decision to breed or defend a territory and would not have been captured in this sample. In addition, birds which may have experienced limiting factors during feather moult may not have survived the winter or returned to breeding grounds and are absent form this sample. Previous studies have shown that up to 25% of nesting attempts are not detected using traditional nest searching methods (McPherson et al. 2003) and undetected attempts may bias results. Since determining the number of fledged young is often estimated, modeled reproductive success and investment may, in fact, be higher.

Corticosterone in feathers is shown to respond to energetic demand during feather growth (Chapter 2) but it is unknown whether these findings can be extended to demands confronted by adult females during moult in the wild. Mallards in prairie Canada are known to be highly mobile and can undertake local post-breeding migrations. I assumed that nesting females captured at St. Denis also moulted wing feather near the same location, and if this assumption was violated then the indices of local conditions may not be appropriate. Additionally, while summer temperatures explained variation in $CORT_f$ for arctic nesting eiders and were presumed to reflect food abundance, relationships between food availability in the prairies are likely not equivalent and alternative environmental parameters may be required to understand limiting sources and energetic constraints, particularly for moulting waterfowl. Although the study sites

selected represented a broad mix of grassland and cropland sites and selected to represent the full range of wetland and upland habitat compositions; indexing other landscape characteristics such as predator communities or food availability would be valuable to inform future studies. Predators are a key driver of reproductive success in waterfowl and may only be weakly captured by site-level variables. While predator foraging patterns and habitat use is tied to specific habitats such as wetland, might explain which greater wetland area results in lower numbers of fledged ducklings (Chapter 5).

I used a novel method to examine components of the hypothesized path diagram. The use of a split process using hurdle models process to jointly assess both the odds and then magnitude of success highlighted a unique manner to tease apart effects on both intrinsic and extrinsic factors. In order to aid comparison of results and strengthen confidence in my interpretations, I also repeated the analysis using the same factors but under a classical structural equation modeling framework and using global fit. Although some of the near-significant paths were removed, all major pathways from the piecewise approach were consistent and retained. This suggests that the relationships identified in this analysis are robust relevant to the method used. Hurdle models break down various components of data that fit alternative distributions. By separating zero and non-zero data and modelling each component individually it is possible to gain insight into component approaches while meeting necessary assumptions for the data. The use of hurdle models may be a more favorable approach to assess datasets with response variables composed of both binary and continuous response measurements. These models may be improved with additional work on developing processes to calculate standardized coefficients and determine relative effects of direct and indirect paths, which would benefit the use of hurdle models in piecewise structural equation modeling frameworks.

The use of hormone biomarkers has potential to index of intrinsic factors, or individual quality, from a physiological perspective. The ability to link individual physiology to conservation or management actions may also provide new perspectives and utility in understanding how population dynamics operate, particularly in modified landscapes (Wikelski and Cooke 2006, Ellis et al. 2012). Overall this study combined the use of landscape and physiologic variables to understand the influences on reproductive success. It highlighted how both broad landscape variables and individual traits work together and counteract each other to impact various components of reproductive success and the ability for individuals to add

variation within the natural environment and amongst landscape levels drivers, advancing knowledge of reproductive trade-offs in prairie-nesting species.

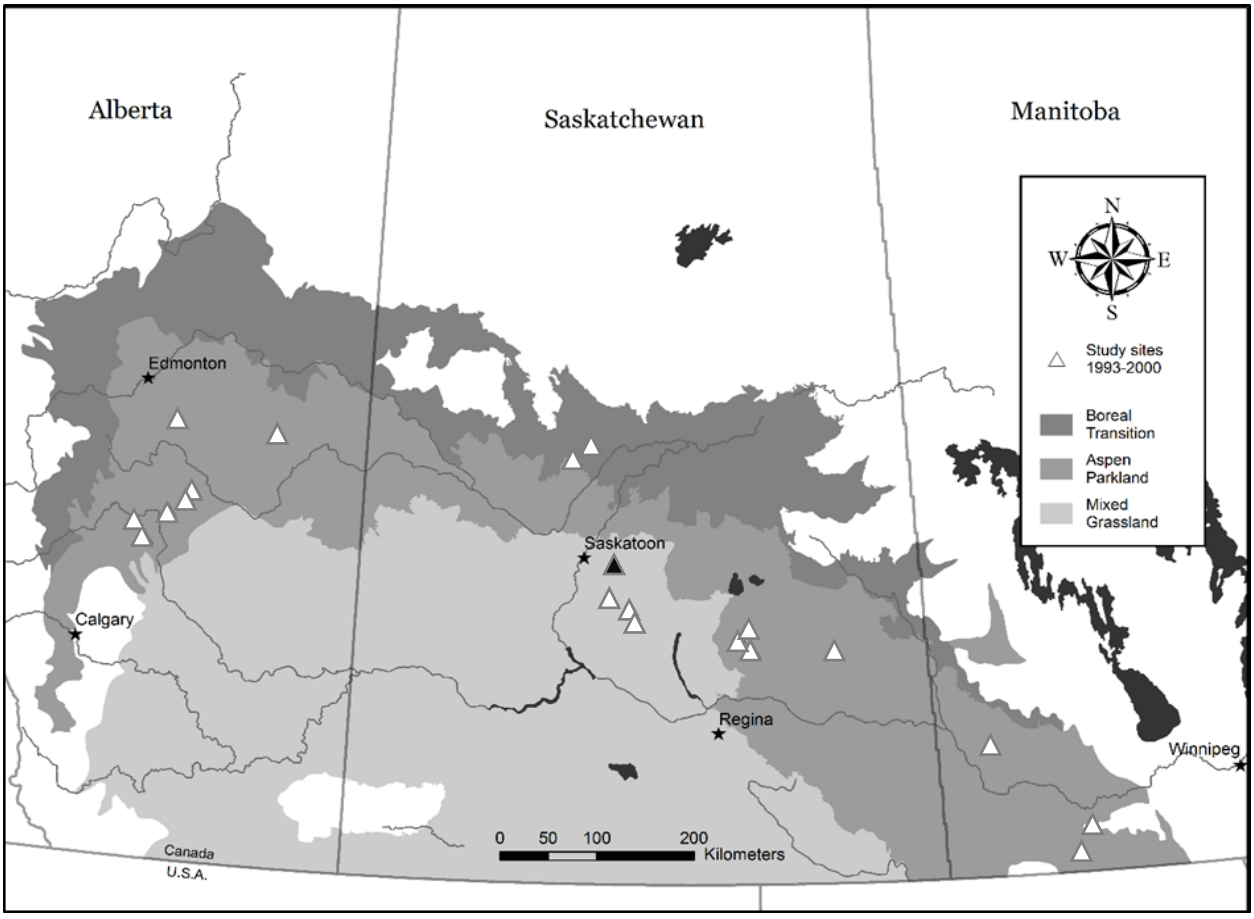

Figure 6.1. Location of study areas used to examine intrinsic and extrinsic sources of variation in mallard reproductive investment and success in the Canadian Prairie Parklands, 1993 – 2000 (white triangle) and at St. Denis National Wildlife Area, 1983 – 2000 (black triangle).

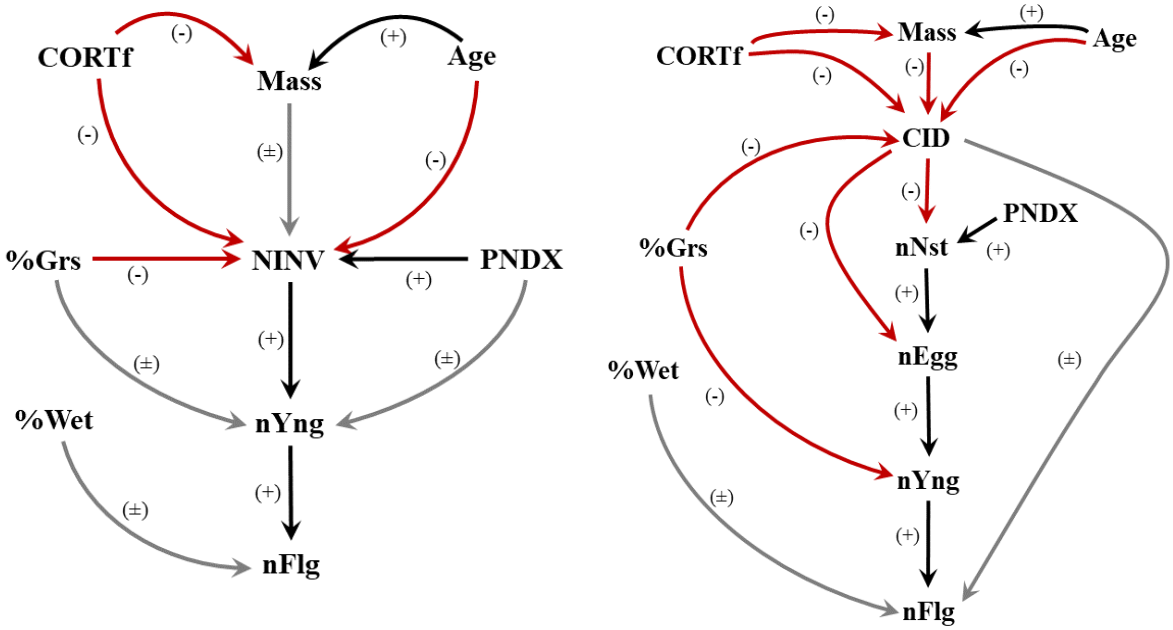

Figure 6.2. Hypothesized path diagrams linking intrinsic condition indices and extrinsic environmental composition to reproductive investment and success in female mallards within the Prairie-Parkland, Canada. Left panel represents model examining all birds including presumed non-nesters. Arrows and symbols indicate the presumed relationships between variables. Right panel represents mallards that initiated at least one nest during the breeding season. Intrinsic variables are body mass (MASS), predicted age (Age), past energetic condition as measured by corticosterone in wing feathers ($CORT_f$) and clutch initiation date of first detected nest attempt (CID); environmental variables are amount of grassland (%Grs), wetland (%Wet) and pond index (PNDX); reproductive parameters are nesting investment index (NINV) and the total number of number of nest attempts (nNst), eggs (nEgg), hatched (nYng) and fledged young (nFlg).

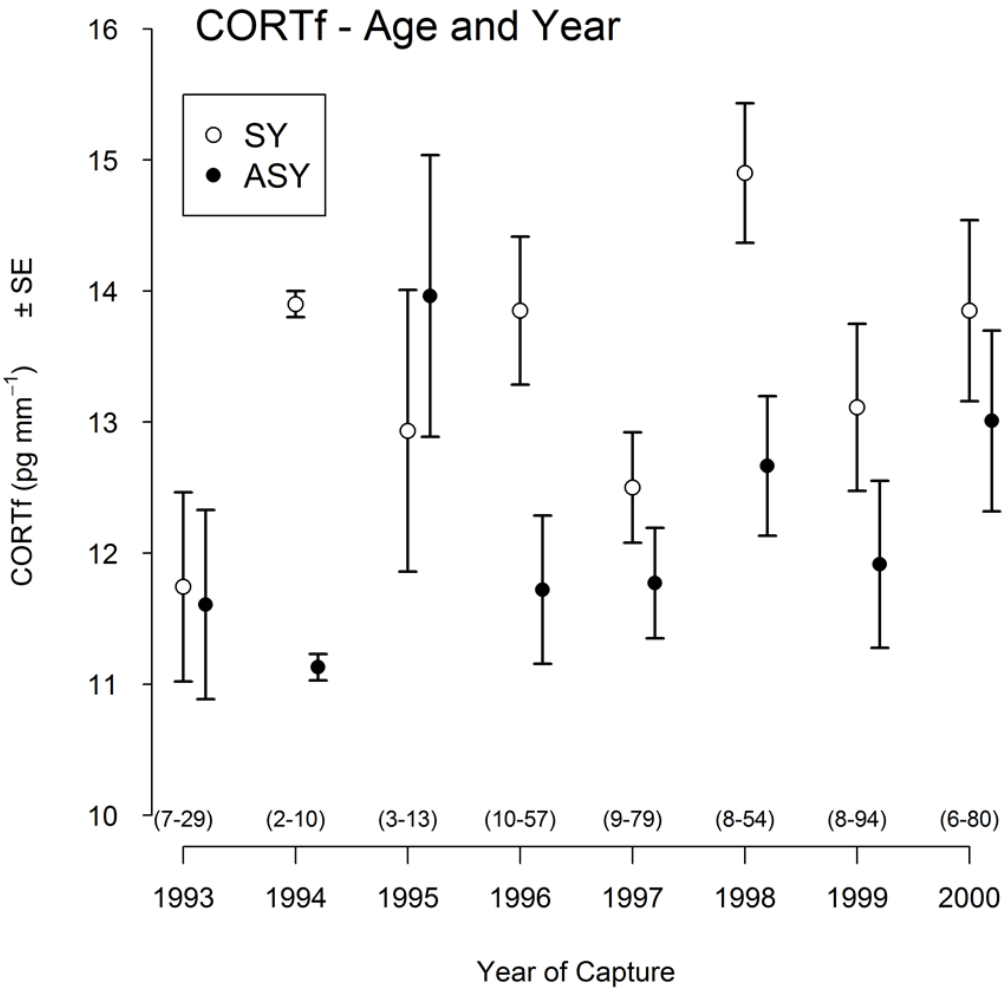

Figure 6.3. Relationship between mean corticosterone (± SE) measured in wing feathers and age cohort (Second Year – open circle; After Second Year – closed circle) of breeding mallards captured in the Canadian Prairie-Parklands between 1993 and 2000. Sample sizes for each category are indicated in brackets immediately above the x-axis.

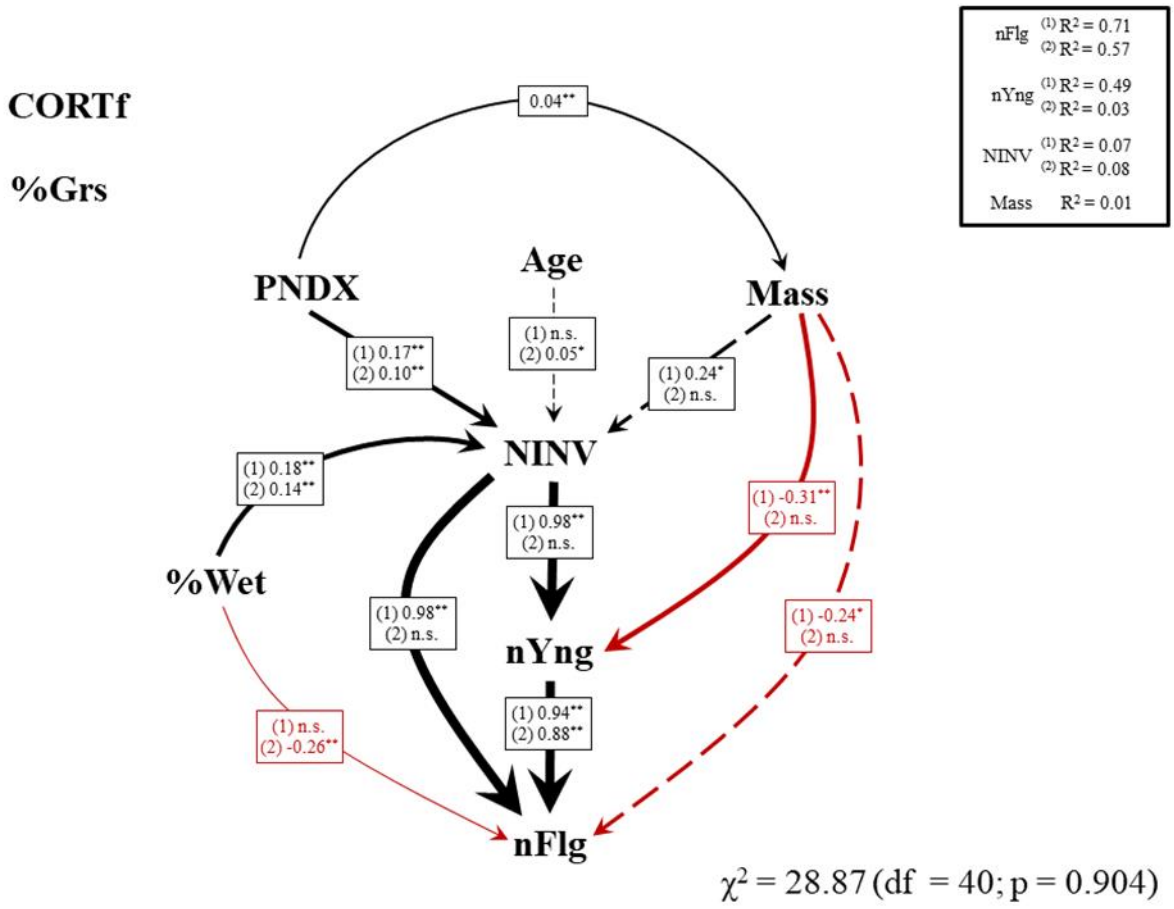

Figure 6.4. Final path diagram for analysis of intrinsic and extrinsic factors that influence breeding or non-breeding and reproductive success for female mallards in the Canadian Prairie Parklands. Red arrows indicate negative coefficients and black arrows are positive relationships. Values indicated next to each path represent the range standardized path coefficients with arrow width indicating relative standardized coefficient value. Where two coefficients are present, each box represents an individual hurdle model where (1) are model zero values using binomial distributions and (2) Poisson or negative binomial distributions for counts greater than zero. Paths that were non-significant but important for overall model fit are also included (n.s.). Solid arrows and coefficients with a double asterisk (**) indicate p-values ≥ 0.05. Dashed arrows and coefficients with a single asterisk (*) indicate p-values less than 0.10. Each model R^2 is presented in the inset box with final model fit in the lower right. Variables included in the model are body mass (Mass), female age (Age), feather corticosterone ($CORT_f$), nesting investment (NINV), proportion of grassland (%Grs), proportion of wetland (%Wet), wetland wetness (PNDX) and total number of young that hatched (nYng) and fledged (nFlg).

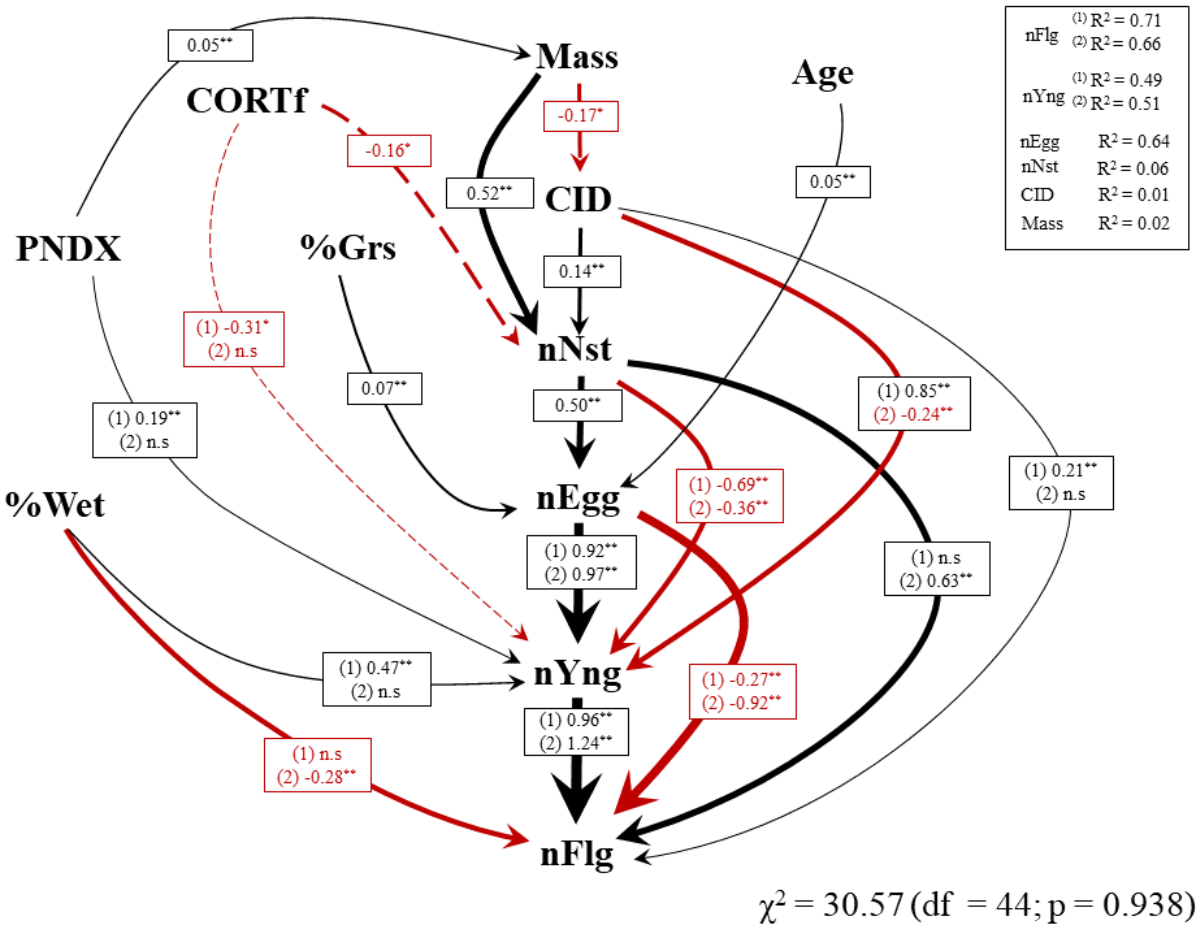

Figure 6.5. Final path diagram for analysis of intrinsic and extrinsic factors that influence reproductive success for breeding female mallards in the Canadian Prairie Parklands. Values indicated next to each path represent the range standardized path coefficients. Where two coefficients are present, each value represents an individual hurdle model where (1) model zero values using binomial distributions and (2) Poisson or negative binomial distributions for counts greater than zero. Paths that were non-significant but important for overall model fit are indicated by an "n.s.". Double asterisk (**) and black color indicate p-values less than 0.05 and single asterisk (*) and dashed arrows indicate p-values less than 0.10. Arrow wide corresponds to standardized coefficient value. Each model R^2 is present in the inset box with final model fit in the lower right. Variable included in the model are body mass (Mass), female age (Age), feather corticosterone ($CORT_f$), proportion of grassland (%Grs), proportion of wetland (%Wet), wetland wetness (PNDX) and total number of nest attempts (nNst), laid eggs (nEgg), and ducklings that hatched (nYng) and fledged (nFlg).

CHAPTER 7: SYNTHESIS

7.1 Summary and Conclusions

The consideration of scale – across space and time – is of central interest in ecology. The location, timing, and mechanisms are determinants of observed variation in both individual reproductive success and habitat selection, and their consideration is essential to ensuring contextual accuracy and relevance (Delcourt et al. 1983, Weins 1989, Fahrig 1992, Turner et al. 2001). Understanding how various spatial and temporal scales interact can be intuitive; from measuring time passage from minutes to months to seasons or visualizing foraging patterns from a specific leaf to tree to patch of forest within the larger landscape. Less intuitive is scaling factors that influence ecological processes such as reproductive success. Within an individual, a cascade of hormones triggers behavioural responses of an individual (e.g., self-maintenance), the acquiring or mobilization of lipid reserves to then extending how that individual interacts with its immediate environment or distant ones over time. Integrating multi-scale approaches to combine spatial, temporal and intra-individual scales as well as their interactions provided a unique context to advance understanding of established theories and evidence while providing opportunity to investigate unresolved ecological questions.

Broadly, my dissertation examined the mechanisms and sources of variation in reproductive success of prairie-nesting ducks using a multi-scale approach (Figure 1.1). I used a combination of manipulations of captive birds as well as observational field studies and existing long-term datasets of wild birds to address questions about variation in reproductive success, including physiologic responses, intrinsic attributes, energetic carry-over effects from prior locations and the structure and composition of the surrounding environment (ranging from habitat patches to a species' range). I tested and validated several established and new assumptions, providing necessary context for the use of hormone biomarkers to index allostatic load in waterfowl; identified mechanisms for carry-over effects from other seasons (i.e., previous summer and winter periods); and addressed several habitat management questions. I identified major drivers of fledging success in prairie-nesting ducks and incorporated knowledge of avian breeding ecology to to explore possible trade-offs between nesting and fledging success for ducks settling in agriculture-dominated environments.

In Chapter 2, I evaluated the use of feather corticosterone ($CORT_f$), an integrated hormone biomarker increasingly being used in conservation and integrative ecophysiology to test for carry-over effects from known challenges occurring in the past. I tested and validated the hypothesized relationship between energy expenditure and $CORT_f$ using experimental manipulations and showed that increasing allostatic load and overload conditions impose negative effects on body condition and growth rate. I demonstrated the ability for $CORT_f$ to record retrospective changes in allostatic load demonstrating changes in body condition were only temporary following reprieve from the energetic challenge while $CORT_f$ was able to retain signatures longer compared to traditional measures body morphometrics.

In Chapter 3, I used a combination of data including banding, direct returns from hunter harvest and continental precipitation maps to assign isotopic signatures of wing and body feathers for pintails. I identified that in 2011and 2012, the majority of pintails moulted wing feathers in the Canadian prairies and highlighted the importance of prairie regions for pintail moult but also demonstrated the larger proportion of birds that originate from boreal and northern latitudes; areas which receive less conservation attention for pintails. I used $CORT_f$ from wing and body feathers to inform interpretations about potential carry-over effects of antecedent energetic conditions from the previous summer (post-breeding) and winter/spring (migration) stages for pintails. I derived predicted locations of feather growth (> 8 months and < 3 months) prior to breeding and despite widespread variation in the assigned provenances of moulting pintails, and corresponding $CORT_f$, I did not find strong evidence that pintail body condition during breeding was related to $CORT_f$ (i.e., energetic profiles) from these periods.

For body feathers, equal proportions of the sample were assigned to Gulf or Pacific coasts and known wintering sites for the species. I did not find major effects of biome, or landscape type from the spring period as influencing subsequent breeding success or nest timing. However, patterns between the nest initiation date of nesting pintails and $CORT_f$ from the spring migratory period warrant further attention as energetic demand may influence timing of nest initiation, a key parameter affecting duckling survival and possibly offspring recruitment. Energy reserves built up on wintering grounds are important for migration and determining the state of individual's upon arrival at breeding grounds. Post-breeding birds face important trade-offs between moult speed and feather quality in order to regain flight capabilities and accumulate adequate fat reserves prior to fall migration. Birds moulting in lower body condition or in poor

quality habitats (i.e. low food abundance) may be energetically challenged, resulting in higher levels of $CORT_f$ in newly grown feathers. Feather moult is also a critical life-history stage, requiring not only large amounts of energy but also in determining annual feather quality. Migrating with lower quality feathers can result in higher energetic demands, delayed arrivals on wintering grounds and possibly reduced survival.

In Chapter 4, I tested whether maternal traits influenced survival of offspring to fledge. Both body condition and hatch date were important predictors, a result consistent with several other studies of nesting waterfowl. This research was also the first, to my knowledge, to examine how potential behavioural traits or syndromes influence offspring survival in ducks. Females which displayed more cautionary behaviour during brood observations tended to raise more offspring. Counter to my predictions, I also found that smaller and later hatching females experienced higher duckling survival rates. This was counter to other studies that have shown higher survival for early hatching and greater recruitment (i.e., first year survival) and opposite of trends established for nests. Beyond crypsis, and predator avoidance with hiding behaviour, smaller females may be more able and willing to devote more resources to brood rearing, a consequence of full commitment to this season's breeding efforts. A contrasting view may be that several of the intrinsic factors were not major drivers of variation in reproductive success and broader environmental pattern have more influence; a question addressed in Chapter 5.

In Chapter 5, I examined how the composition and configuration of agricultural environments influences pintail duckling survival and contrasted survival rates between grassland- and cropland-dominated landscapes. The number of duckling survival studies for pintails in the literature is limited and due to conservation needs, survival estimates for grassland- and cropland dominated landscapes was required. My research compared duckling survival rates in both landscape types in two different years and confirmed that survival was lower in crop-dominated landscapes, estimates that are of value to conservation managers and reinforces the importance of retaining native grassland environments to support prairie bird populations. I also examined habitat specific differences at management-relevant scales and showed that perennial cover and winter wheat supported similar survival rates, well above those recorded for broods raised in spring-seeded croplands. Winter wheat provided a supportive role for duckling survival and the gains made through enhanced nest survival recorded in fall-seeded croplands. The survival trade-off between high nesting success and low duckling survival in

cropland landscapes was not supported and based on preliminary estimates, I demonstrate how fall expansion in fall-seeded croplands can benefit nesting and brood-rearing pintails. Finally, I examined relationships between local habitat configuration and composition, and found positive associations between duckling survival, the abundance of seasonal wetlands and area of perennial cover. These findings confirm that retaining native grasslands and small wetlands are important conservation objectives for the region. I show that the configuration of wetlands, and specifically, as the amount of wetland edge increased, duckling survival was reduced. The combination of positive effects of seasonal wetlands and negative effects of wetland edge suggests a trade-off may occur between numerous small seasonal wetlands compared to large basins. Wetlands with high ratios of edge to interior may expose duckling to increased risks of predation while larger ponds have the greatest total amount of edge. If pintail ducklings can stay within cover and away from the outer edges, thereby utilizing intermediate sized wetlands then wetland configuration may assist in providing survival benefits. Although several methodological challenges inhibit my full examination of the implications for duckling survival on large basins, the conservation of grassland landscapes with abundant seasonal wetlands, perennial cover and a variety of small to intermediate sized basins appears robust to ensuring a variety of functional brood rearing habitat is available.

In Chapter 6 I used an existing long-term dataset to extend the investigation of the causes of variation in $CORT_f$ to determine if signatures in feathers were in response to breeding effort or environmental temperature or precipitation as suggested in other studies. Using a unique multi-year mark-recapture dataset I was able to not only collect detail reproductive information on individuals at multiple points in time as well as have a feather collected from at least the first period. I did not find any evidence that $CORT_f$ was responding to breeding effort, success, summer temperatures or wetland conditions. The variation within $CORT_f$ did suggest that energetic demands did occur during feather growth, but effects of interest were not supported. This result suggests that the metrics chosen were either not indicative of energetic response or the timing of those events did not overlap or have lasting effects. I also examined downstream response through a carry-over effects and found a similar lack of explanatory power.

I then combined information from one of the largest datasets of mallard reproductive success in Canada and examined the interactions between intrinsic and extrinsic sources on reproductive effort and success. Waterfowl settling in the prairies and parklands must make

breeding decisions to select landscapes for breeding and the degree if investment. I showed the importance of female body mass in not only facilitating the landscape that were used, but also in making breeding decisions to nest or not. While mass was a positive factor for nesting, there appeared to be a trade-off with hatching and fledging success, a similar result found across multiple chapters. I also showed the importance of wetlands in a landscape and favorable hydrologic conditions. I then examined birds that attempted breeding to see if the patterns held up or new ones emerged and again found evidence that female body mass was influential along with wetland conditions having positive effects on nesting but trade-offs with fledging success.

Overall, several patterns emerged from my research. In prairie-nesting waterfowl, energetic demand still plays a role in determining not only nesting success but success of offspring as well. However, it does not appear as though continental populations of pintails and mallards are heavily influenced by energetic carry-over effects from up to a year prior to the same degree as seabirds and arctic-nesting waterfowl or shorebirds. The broad drivers of variation in reproductive success largely and consistently fall to habitat and landscape composition and for duckling survival, the water conditions on that landscape. While intrinsic factors do cause variation in survival rates, the retention of high-quality habitats will have lasting effects to benefit avian reproductive success.

7.2 Future Research

Despite the allostatic load hypothesis being validated in Chapter 2, several unanswered questions remain regarding the interpretation of $CORT_f$ in wild birds. For studies like that of wild female mallards in Chapter 6, returning birds are survivors that moulted successfully, over-wintered and returned the subsequent year; $CORT_f$ levels of non-survivors and nonbreeders may be quite distinct. In Chapter 6 I had a unique opportunity to look at whether reproductive effort or environmental factors drive variation in $CORT_f$, but the selected variables did not explain significant variation and the main drivers of $CORT_f$ remain elusive for this and other prairie-breeding species. An outstanding challenge of using $CORT_f$ remains understanding which events lead to elevated $CORT_f$ levels and whether this has any effect on components of fitness.

Waterfowl present an excellent opportunity to further test assumptions related to energetic expenditure and $CORT_f$ as wing feathers are moulted simultaneously during brood-rearing or following breeding. Additional work to characterize energetic demands during wing

feather moult would be of great benefit. Collection of movement rates and fine scale location data would not only benefit our understanding of post-breeding life stages such as moult and fall migration but assist in understanding $CORT_f$ ecology. Additionally, the use of experimental manipulations during the post-breeding period could also test additional assumptions for this work in the future (i.e., manipulations of clutch and brood sizes, food availability, etc.).

Results from Chapter 3 identified potential carry-over effects of $CORT_f$ influencing reproductive timing of pintails and could be examined directly in future studies. By focusing the analyses on breeding individuals, a large cohort of individuals were not sampled, including birds that chose to defer breeding (i.e., non-breeders) and those that were incapable of breeding (e.g. health, starvation, death, etc.). Thus, additional variation in ages and body conditions were missing from the sample. Unresolved questions remain on the mechanisms for individuals to forgo breeding, flyover or shortstop migration and if that portion of the population is restricted from breeding, and likewise if birds that fail early have intrinsic conditions that limit their chances of being successful. It is the lagging tail of the distribution of breeding individuals that may provide a more complete picture towards the applicability of carry-over effects. Studies that mark and follow birds from wintering to breeding grounds and/or capture individuals immediately upon arrival and then monitor subsequent reproductive attempts and non-attempts would be valuable.

Results from Chapter 5 highlighted the potential benefits that winter wheat could play for increasing pintail productivity. I presented a cursory calculation demonstrating the benefits of expanding winter wheat production and potential gains for pintail nests and broods. Efforts to characterize duckling survival (and hen success), across a variety of species and landscapes would be useful to strengthen the rationale for winter wheat expansion. While landscape-level manipulations are difficult, altering the amount of winter wheat on the landscape and testing for expected productivity gains would be informative. With increasing agricultural intensification, there will be continued pressure on native grasslands and seasonal wetlands for conversion to intensive agriculture. The adoption of some alternative agriculture and agroecology practices may also benefit pintails through similar processes as fall crops (e.g., retain cover crops, land idling, and alternative rotation schedules, etc.). Collaborative efforts which work towards large landscape-level manipulations in concert with studies of pintail productivity and recruitment would be highly relevant and informative to pintail habitat conservation efforts.

Table 7.1. Summary of tested hypotheses, relevant scale(s), variables of interest, predictions and key findings. Solid squares indicate whether results were consistent (■), open squares as not consistent (□), or split squares as partially consistent (◩) with predictions.

Chapter-specific Tested Hypotheses			
Response	**Explanatory**	**Predictions**	**Key Findings**
CHAPTER 2			
H2.1: Experimental increases in workload alter energy expenditure and allostatic load, modulated through body condition, growth and hormones. (Physiology)			
Body Mass	Workload, Body Mass (initial)	Body mass declines with increased allostatic load	■Body mass declined in workload treated groups relative to unencumbered ducklings; however, effects were damped in older ducklings as body mass was lower for the combined workload group only.
Growth Rate	Workload, Body Mass (initial)	Growth rate slows with increasing allostatic load	■Growth rates were lower in treated ducklings.
Daily Energy Expenditure	Workload, Body Mass	DEE is higher in workload induced birds	■ Daily energy expenditure was higher in bird carrying loads over obstacles relative to controls.
$CORT_f$	Workload (Past & Current)	$CORT_f$ increases with allostatic load relative to controls, with the highest levels in combined workload group	■ $CORT_f$ reflects current energetic demands during feather replacement; however, effects are reduced in older ducklings.
H2.2: $CORT_f$ reflects total energy demands during, and prior to feather growth. (Physiology)			
$CORT_f$	Workload (current & past), $CORT_f$ (past)	$CORT_f$ is positively related to current and past workloads	◩ $CORT_f$ reflects current workload but is positively influenced by antecedent glucocorticoid levels, particularly for birds with over-elevated responses.
CHAPTER 3			
H3.1: Regional differences in moult location affect energetic demand modulated through $CORT_f$, that have downstream impacts on indicators of reproductive success. (Landscape to Continental)			
Wing feather isotopic signatures (H, N, C, S)	Year, Female Age, Landscape	No differences between ages, landscapes but differences between years due to annual breeding distribution.	■ Pintails nesting in 2011 had a lower mean $\delta^{2}H$ values and higher $\delta^{34}S$ compared to birds captured in 2012. □ Birds nesting in grassland landscapes had lower mean $\delta^{15}N$ values compared to cropland landscapes.

			◩ Pintail wing feathers did not differ in $\delta^{13}C$ between years, ages or landscapes. ■ Pintails nesting in 2011 had a lower mean $\delta^{2}H$ values compared to 2012. ◩ Variation in $\delta^{13}C$, $\delta^{15}N$ or $\delta^{34}S$ isotopes from body feathers did not differ between ages, breeding landscapes, or years.
Body feather isotopic signatures (H, N, C, S)	Year, Female Age, Landscape	No differences between ages or landscapes but differences between years due to flyway and wintering prevalence.	
H3.2: Variation in $CORT_f$ as a result of regional energetic differences between moult locations act as negative carry-over effect on female body condition and timing of nest initiation. (Physiology to Continental)			
$CORT_f$	Female Age, Landscape, Biome, Latitude ($\delta^{2}H$)	$CORT_f$ in wing and body feathers will differ between ages, landscape and biomes.	◩ Wing feather $CORT_f$ was higher in adults than juveniles but did not differ between summer landscape type, biome or $\delta^{2}H$. ■ Body feather $CORT_f$ was higher for birds predicted from more southern latitudes □ Body feather $CORT_f$ did not differ between ages, landscape types or biomes.
Body Condition	Winter Biome, Winter Aquatic, $CORT_f$, Arrival	Body condition differs based on the predicted wintering region and arrival date with early arriving birds in greater condition.	□Variation in body condition was not explained by included variables.
Nest Initiation	Body Condition, Landscape, Biome, CORTf	Nest initiation date differs between predicted wintering region where earlier breeding birds are in higher body condition and have lower $CORT_f$ values	◩ Birds that nested later in the season had higher levels of $CORT_f$ in body feathers or came from coastal regions during winter or spring migration.
CHAPTER 4			
H4.1: Variation in intrinsic condition, maternal traits and reproductive timing influence resources allocations to parental care and reproductive performance for northern pintails in prairie environments. (Individual)			
Duckling Survival	Age, Body Condition, Behaviour, Hatch Date	Females which are older, in higher body condition, more cautious, and breed earlier have higher offspring survival rates.	□ Duckling survival was higher among female pintails with lower body mass, those that hatched nests somewhat later in the season and not related to female age. ■ Duckling survival was higher among female pintails that behaved more cautiously during brood rearing.

CHAPTER 5			
H5.1: The loss and alteration of waterfowl nesting and brood-rearing habitats due to agricultural intensification have led to reductions in pintail duckling survival rates.in cropland-dominated landscapes. (Landscape)			
Duckling Survival	Landscape, Duckling Age, Hatch Date, Site/Year	Duckling survival rates are lower in annual cropland-dominated landscapes	■ Cumulative 30-day survival is lower in cropland-dominated landscapes relative to grassland-dominated landscapes □ Duckling which hatched later in the season had higher survival rates.
H5.2: A survival trade-off exists between higher nesting success in winter wheat offsetting costs of lower duckling survival in cropland landscapes and confer survival advantages due to earlier hatch dates. (Habitat)			
Duckling Survival	Nesting Habitat, Duckling Age, Hatch Date, Site/Year	Duckling survival rates are highest for broods originating from perennial cover and winter wheat relative to spring-seeded cropland.	■ Cumulative survival rates were lowest for ducklings from nests in spring-seeded cropland but comparable between perennial cover and winter wheat. ◩ No trade-off was detected between early hatching in winter wheat and lower survival in cropland landscapes. □ Duckling which hatched later in the season had higher survival rates.
H5.3: Variation in the extrinsic environment, including the composition and configuration of brood habitat, influences survival rates of pintail ducklings. (Habitat)			
Duckling Survival	Composition, Configuration, Duckling Age, Hatch Date, Site/Year	Areas with abundant and high densities of wetlands, or abundant grassland will have higher duckling survival rates.	◩ Higher proportions of seasonal wetlands and perennial cover had positive survival effects, while higher densities of wetland edge had a negative effect on survival. □ Duckling survival did not differ between hatch dates.
CHAPTER 6			
H6.1: Female body condition and $CORT_f$ levels in wing feathers are a product of the energetic demands of recent breeding performance and/or environmental conditions immediately prior to feather growth. (Physiology, Individual and Landscape)			

$CORT_f$	<u>Intrinsic</u> Female Age, Body Condition, Nest Initiation, Clutch Size, Brood Size, Days Brood-rearing <u>Extrinsic</u> Air Temperature, Wetland Abundance, Pond Index, Year	Birds with experience or in higher body condition may have lower $CORT_f$ due to better habitat selection or condition Larger clutch, brood size or extended brood-rearing periods increase energetic demand and $CORT_f$ Higher temperatures, low water conditions or reduced pond abundance may increase energetic demand during moult and $CORT_f$	□ Variation in $CORT_f$ was not related to either intrinsic female traits (body condition, structural size) or reproductive effort (clutch size, brood size or length of brood rearing). □ Measured environmental conditions (summer air temperature, precipitation, wetland abundance or water conditions) did not explain significant variation in $CORT_f$.
Body Condition	$CORT_f$	Birds with higher $CORT_f$ in wing feathers arrive on breeding grounds in lower body condition the following year.	□ No support for carry-over effect of prior $CORT_f$ from wing feathers grown in summer-fall the previous year on body condition in the following year.
H6.2: Both past and current intrinsic factors with current landscape composition influence avian reproductive decisions. (Individual to Landscape)			
Body Condition	Pond Index	Females in higher body condition should be older and have lower $CORT_f$,	■ For breeding mallards, heavier females were more likely to settle in areas with above average wetland conditions
Nesting Investment	Female Age, Female Mass, Pond Index, Wetland Abundance	Females that should choose to breed are likely older, more experienced, in good condition and select favorable habitats	□ Lighter females are less likely to breed but experienced higher hatching and fledging success. □ Female age had no direct effects on the decision to breed nor directly influenced fledging success.
Hatched Young	Nest Investment, Female Mass	Females that have higher hatching success select favorable habitats	■ Greater nesting effort occurred on sites with a higher abundance of ponds and above average wetland conditions.
Fledged Young	Nesting Investment, Wetland Abundance, Female Mass	Females that have higher fledging select habitats with high wetland abundance.	□ Reproductive success was unrelated to $CORT_f$ levels in feathers grown the previous summer-fall. □ Composition of grassland did not appear to be an important factor in determining breeding for mallards

H6.3: Both past and current intrinsic factors with current landscape composition influence avian reproductive investment and success. (Individual to Landscape)			
Body Condition	Pond Index	Females in higher body condition should be older and have lower energy demands ($CORT_{f,}$)	■ For breeding mallards, heavier females were more likely to settle in areas with above average wetland conditions.
Clutch Initiation	Female Mass	Females that nest earlier will be older, in good condition and have lower $CORT_f$.	◩ Heavier females were more likely to nest earlier and more often while females which were older or settled in areas with more grasslands, had larger clutch sizes.
Nesting Attempts	Female Mass, Clutch Initiation, $CORT_f$	Females will invest more into re-nesting under favorable habitat conditions for brood-rearing.	◩ Birds with lower $CORT_f$ in wing feathers re-nested more and experienced higher hatching success as did females that delayed nesting or nested on sites with lower pond abundances.
Clutch Size	Female Age, Grassland Abundance	Clutch size and re-nesting declines throughout the season	◩ Brood size at hatch was smaller for late or re-nests; yet, fledging success increased in late-hatched broods.
Hatched Young	Clutch Initiation, Nesting Attempts, Clutch Size, Wetland Abundance, Pond Index	Nests in grassland landscapes have higher hatching success	■ The number of fledged ducklings per brood was positively associated with wetland abundance.
Fledged Young	Clutch Initiation, Nesting Attempts, Clutch Size, Wetland Abundance	Fledging success and duckling survival are highest early in the season and in landscapes with abundant wetlands	□ Increased re-nesting elevates odds of successful hatching or fledging but diminishes returns through lower hatching success and smaller broods beyond seasonal clutch size reductions.

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APPENDIX A: CAPTIVE MALLARD EXPERIMENT SUPPORTING INFORMATION

This was reprinted from: Johns, D. W., T. A. Marchant, G. D. Fairhurst, J. R. Speakman, and R. G. Clark. 2017. Biomarker of burden: Feather Corticosterone reflects energetic expenditure and allostatic overload in captive waterfowl. Functional Ecology 32:345-357, with permission from

Table A.1. Mallard (*Anas platyrhynchos*) greater secondary covert wing feather length (mm) and mass (mg) summary data by workload treatment for phases one and two.

Phase	Age	Group	N	Length ± SE	Min - Max	Mass ± SE	Min - Max
One	57 days	Cc	17	59.7 ± 0.7	(56 – 66)	24.5 ± 0.6	(20.6 – 30.1)
		Cw	20	59.6 ± 0.8	(52 – 64)	24.3 ± 0.6	(18.8 – 27.9)
		Tc	19	58.9 ± 1.0	(51 – 67)	24.3 ± 0.5	(20.0 – 30.0)
		Tw	19	57.2 ± 0.8	(52 – 62)	22.6 ± 0.5	(17.9 – 26.9)
Two	133 days	Cc	19	63.0 ± 0.8	(57 – 73)	26.9 ± 0.6	(23.6 – 32.1)
		Cw	17	60.9 ± 0.7	(56 – 66)	25.8 ± 0.7	(20.3 – 31.0)
		Tc	20	60.4 ± 0.4	(57 – 63)	26.0 ± 0.4	(23.3 – 28.6)
		Tw	19	60.4 ± 0.6	(56 – 66)	25.5 ± 0.6	(22.0 – 31.0)

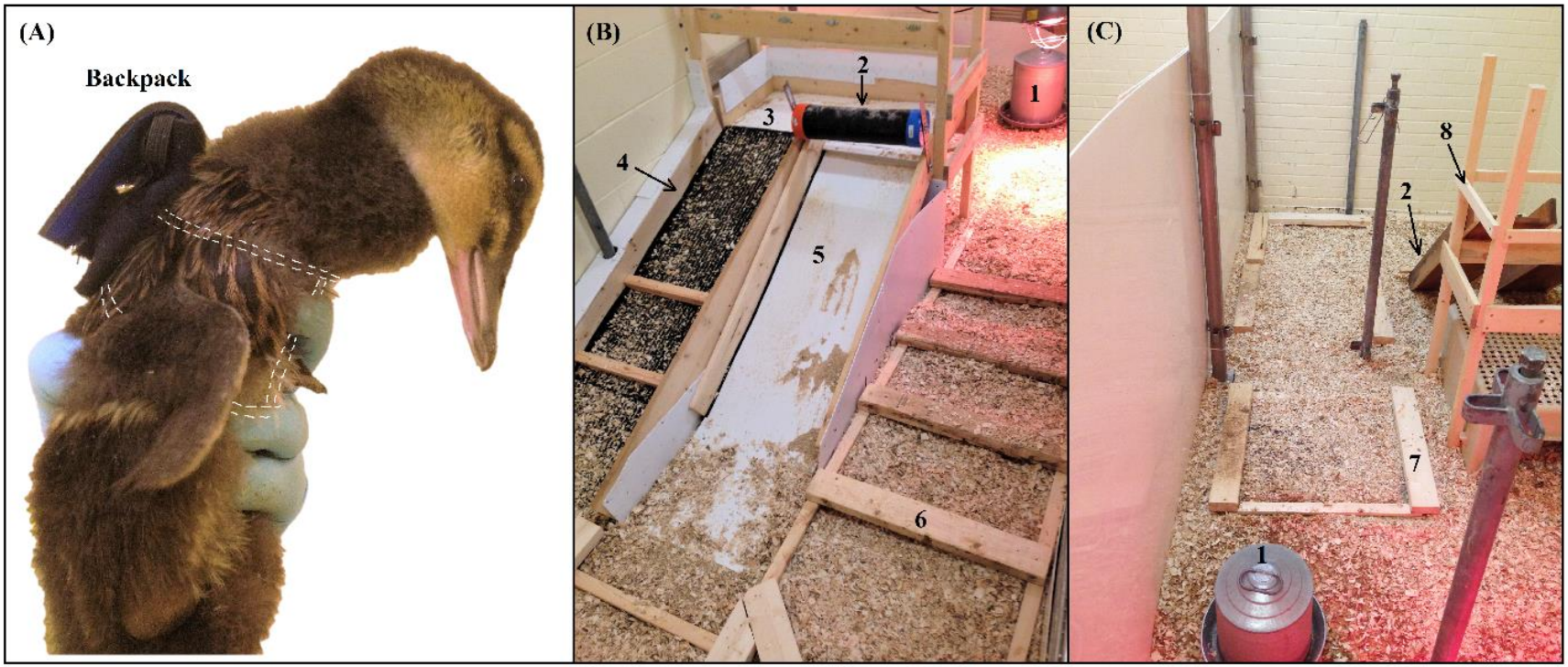

Figure A.1. Experiment design - this study examined whether increases in daily workload were reflected in feather corticosterone levels in female mallard (*Anas platyrhynchos*) ducklings. Birds were subjected to workload treatments using physical obstacles and/or carrying back-mounted weights (Panel A) weighing approx. 10-18% of body mass to increase energetic expenditure. White dashed lines in panel a indicate where elastic straps were positioned to secure neoprene backpack. Each room was separated into two pens (Panels B and C) using a divider and half of ducklings in each pen carried backpacks (weight treatment). All birds had unlimited access to food and water (#1). Tower treatment pens (Panel B) had feeders (#2) on an adjustable height platform (#3), accessed by a ramp (#4) and slightly suspended over a slide (#5). Ducklings were forced to traverse obstacles (#6) and climb the access ramp before descending the slide or returning down the ramp. Control pens (Panel C) had both water (#1) and food (#2) placed at ground level. Sham obstacles (#7) and towers (#8) controlled for enrichment and spacing effects.

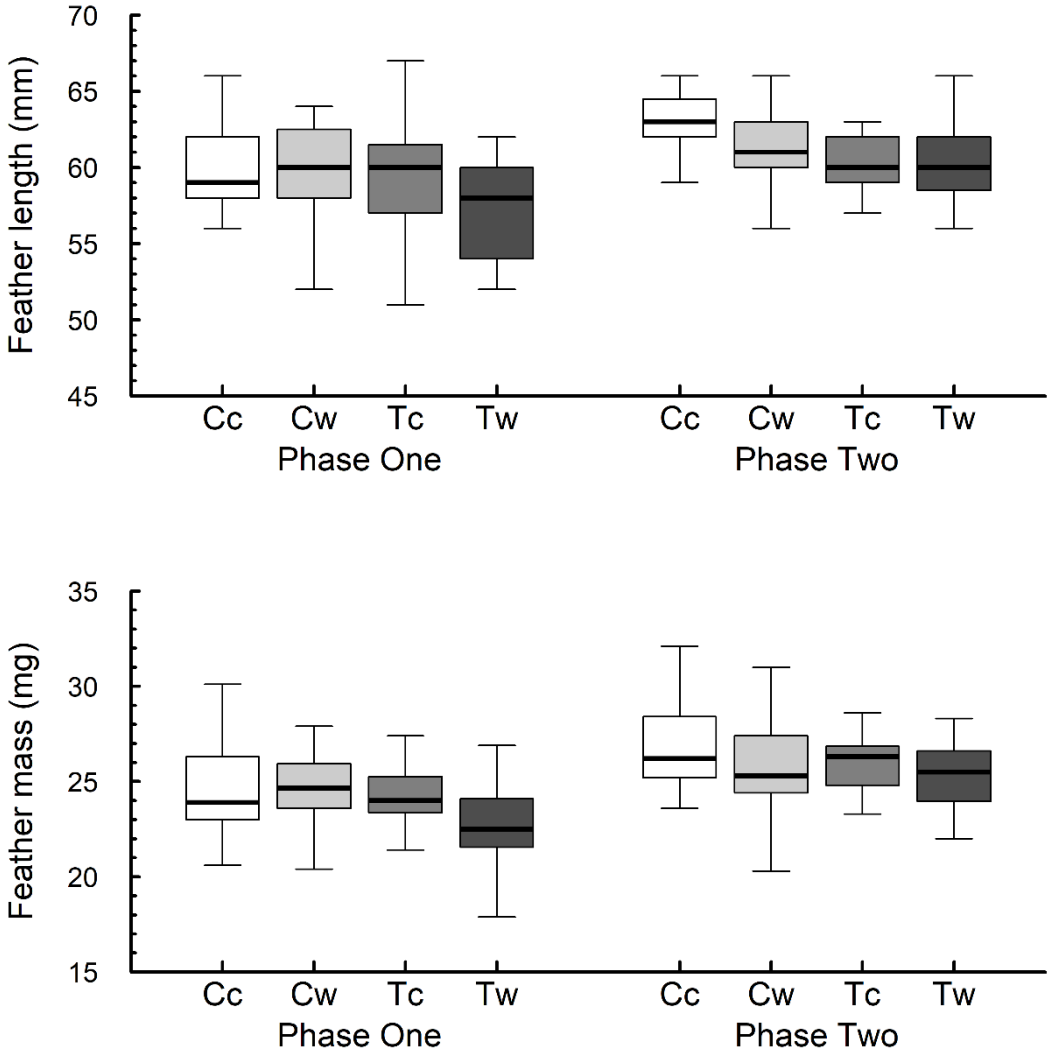

Figure A.2. Distribution of greater secondary covert wing feather length (mm) and mass (mg) measurements collected from mallards (*Anas platyrhynchos*) for each treatment group in phases one and two. Boxplots show median (horizontal line within boxes), lower and upper quantiles (bottom and top lines of boxes, respectively) and minimum and maximum values (lower and upper horizontal lines, respectively). Significant differences in feather length and mass only are found between treatment Cc and Tw. Sample sizes shown in Table A.1.

APPENDIX B: STABLE ISOTOPE ANALYSIS OF NORTHERN PINTAIL WING AND BODY FEATHERS SUPPORTING INFORMATION

Table B.1. QAQC for stable isotope analysis of wing (greater secondary covert) and body feathers from female northern pintails (*Anas acuta*) nesting in southern Saskatchewan, between 2011 and 2012.

Isotope	Standard (Type)	Reference (‰)	Wing (Mean ± SD)	Body (Mean ± SD)
$\delta^{2}H_{VSMOW}$	Polyethylene powder	-100.3	-65.0 ± 0.6	-75.64 ± 2.80
	KHS Hair	-54.1	-54.1 ± 0.7	-53.22 ± 2.57
	BWB Baleen	-108	-110.9 ± 1.0	-109.57 ± 1.80
	CBS Keratin	-197	-197.0 ± 0.8	-196.30 ± 1.85
	Chx Keratin		-109.2 ± 1.3	-106.49 ± 1.90
$\delta^{13}C_{VPDB}$	G-13 Bovine Liver	-21.69	-21.65 ± 0.02	-21.50 ± 0.00
	G-17 USGS-41 Glutamic Acid	37.626	37.61 ± 0.10	37.63 ± 0.09
	G-18 Nylon 5	-27.72	-27.72 ± 0.05	-27.72 ± 0.03
	G-9 Glutamic Acid	-28.85	-28.93 ± 0.06	-29.02 ± 0.05
$\delta^{15}N_{Air}$	G-13 Bovine Liver	7.72	7.90 ± 0.00	7.63 ± 0.00
	G-17 USGS-41 Glutamic Acid	47.6	47.60 ± 0.07	47.60 ± 0.02
	G-18 Nylon 5	-10.31	-10.31 ± 0.07	-10.30 ± 0.10
	G-9 Glutamic Acid	-4.26	-4.09 ± 0.07	-4.10 ± 0.05
$\delta^{34}S_{VCDT}$	IAEA S-1 Baleen	18.15	18.14 ± 0.23	18.46 ± 0.25
	IAEA S-2 Hair	1.91	2.49 ± 0.18	2.49 ± 0.43
	IAEA S-3 Taurine	-3.94	-3.32 ± 0.16	-3.92 ± 0.39

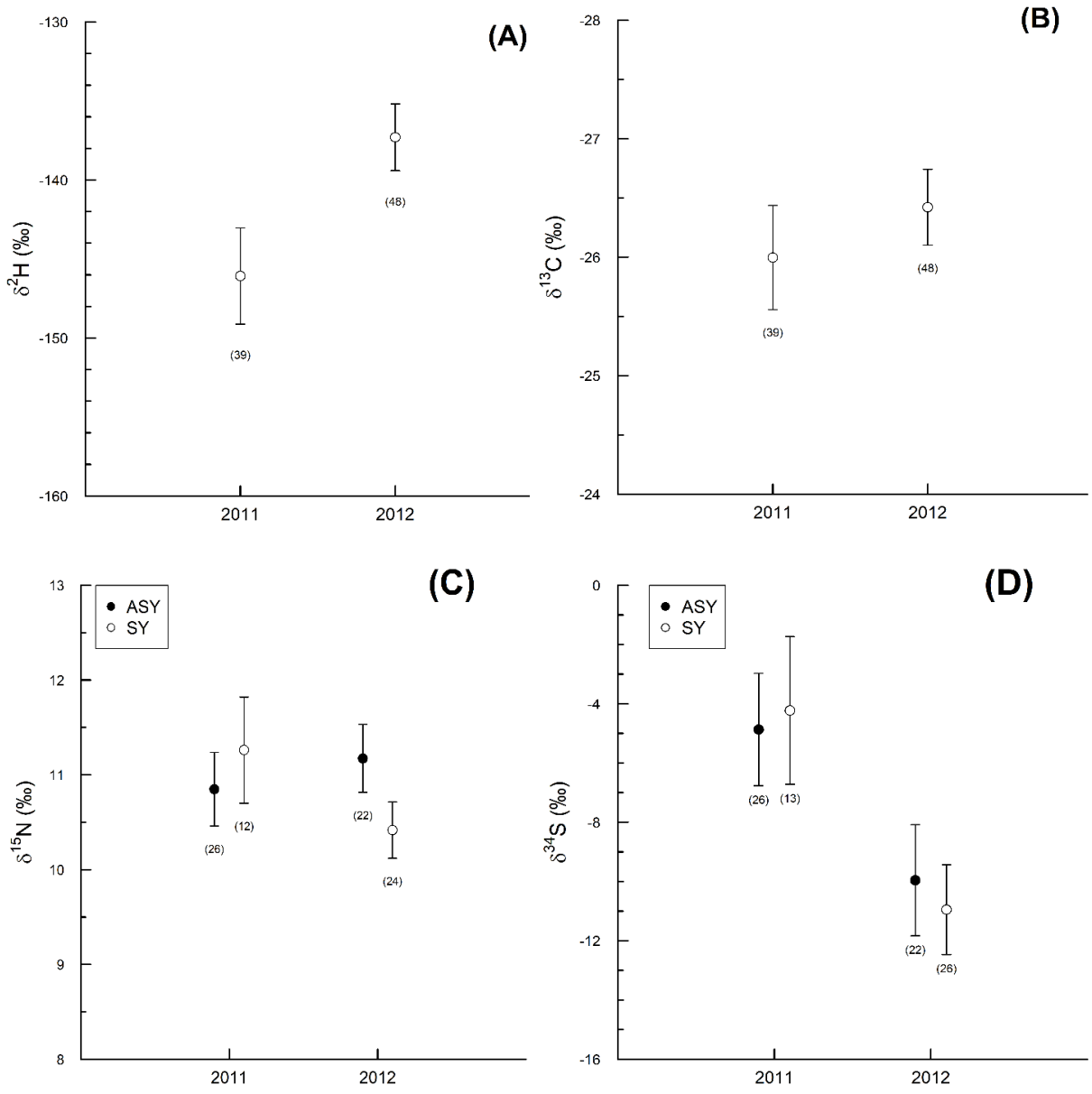

Figure B.1. Distribution of stable isotopes (‰) of hydrogen (δ 2H; panel A), carbon (δ 13C; panel B), nitrogen (δ 15N; panel C) and sulphur (δ 34S; panel D) measured in wing feathers from female northern pintail breeding in southern Saskatchewan, 2011 – 2012. Adult female (black dots) and first-time breeders (white dots) separated within each year.

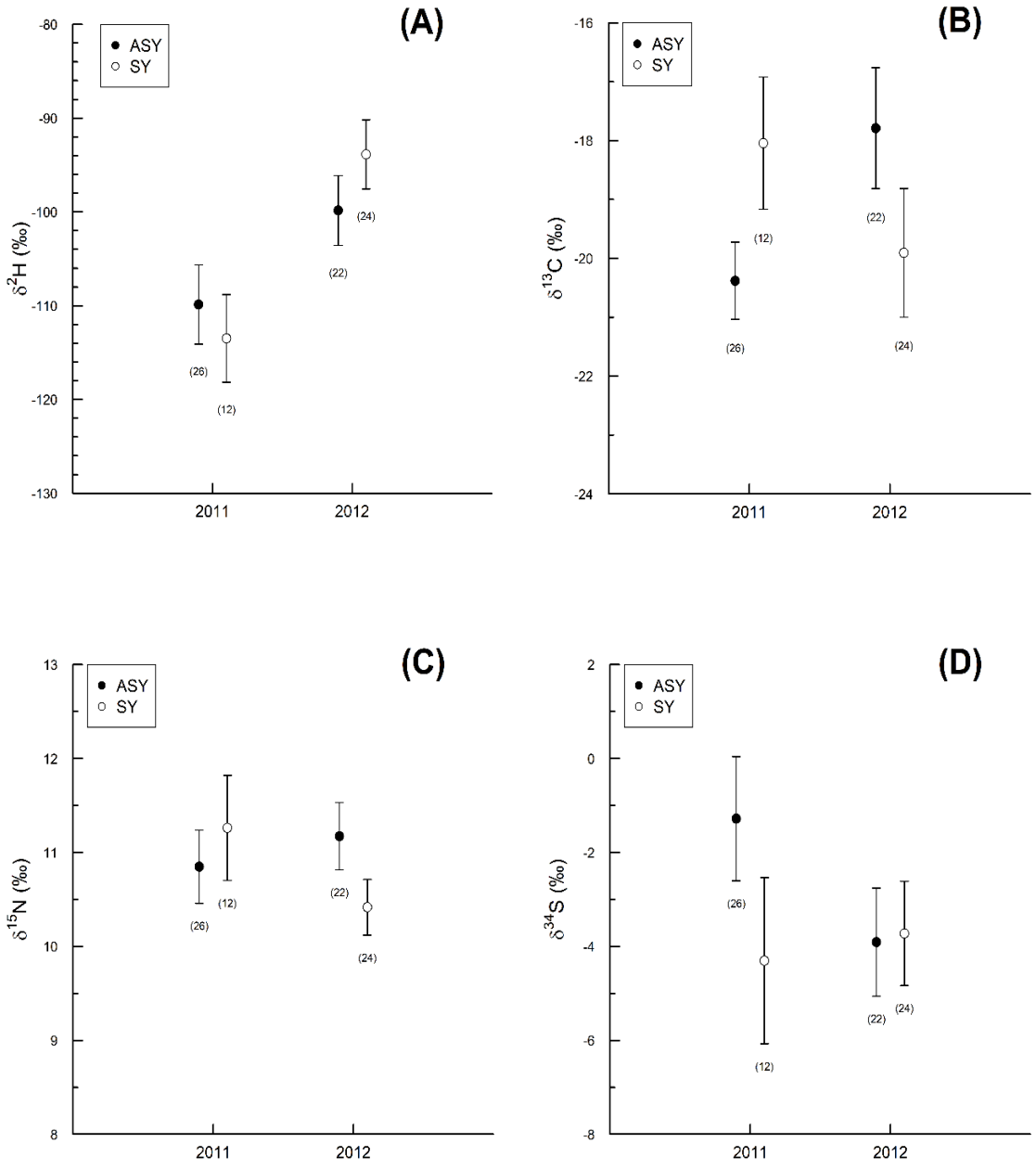

Figure B.2. Distribution of stable isotopes (‰) of hydrogen (δ 2H; panel A), carbon (δ 13C; panel B), nitrogen (δ 15N; panel C) and sulphur (δ 34S; panel D) measured in body feathers from female northern pintail breeding in southern Saskatchewan in years 2011 and 2012. Adult female (black dots) and first-time breeders (white dots) separated within each year.

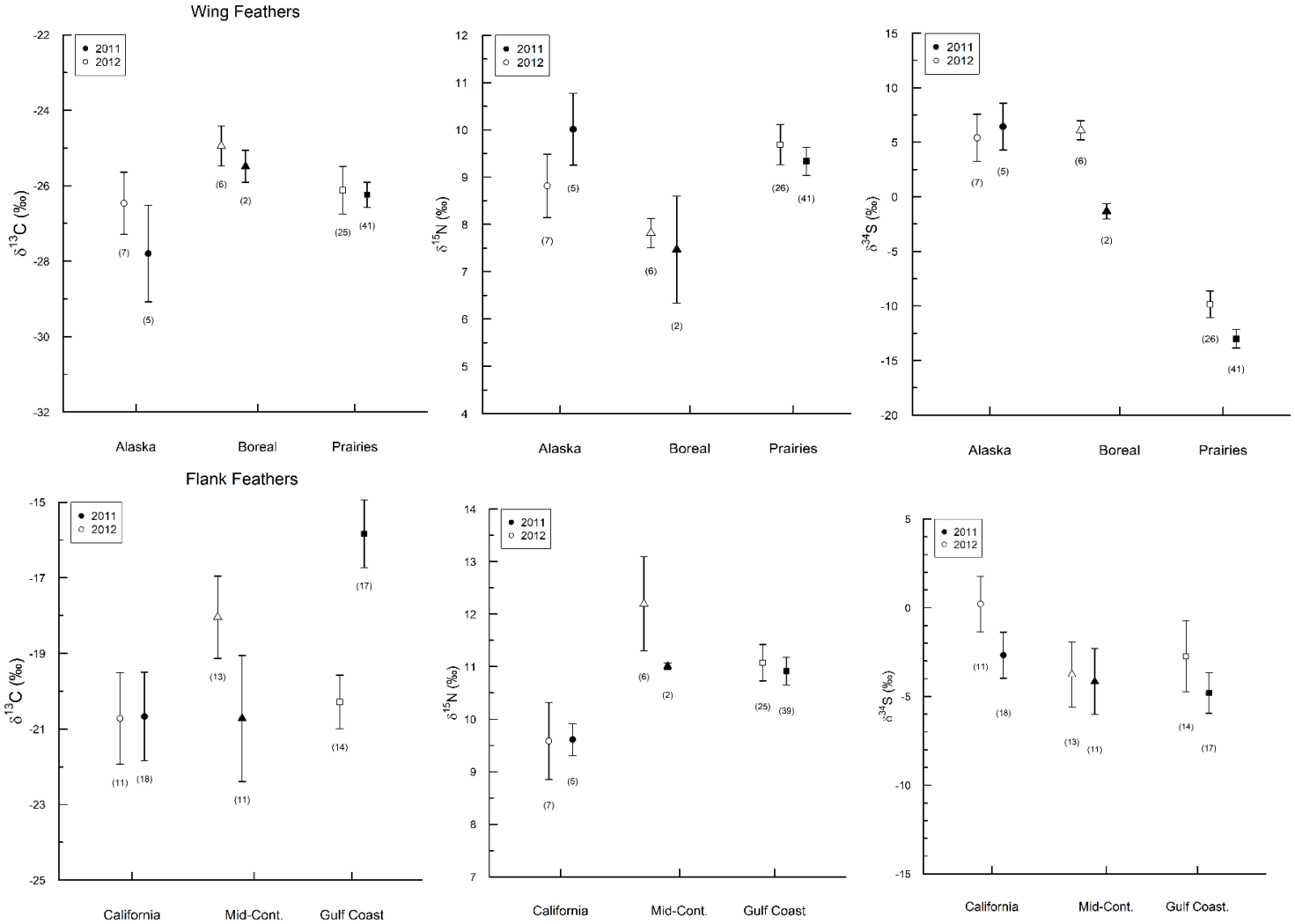

Figure B.3. Distribution of stable isotopes (‰) of carbon (δ ^{13}C; left panels), nitrogen (δ ^{15}N; center panels) and sulphur (δ ^{34}S; right panels) measured in wing (upper) and body (lower) feathers from female northern pintail breeding in southern Saskatchewan in years 2011 and 2012. Adult female (black dots) and first-time breeders (white dots) are separated within each year

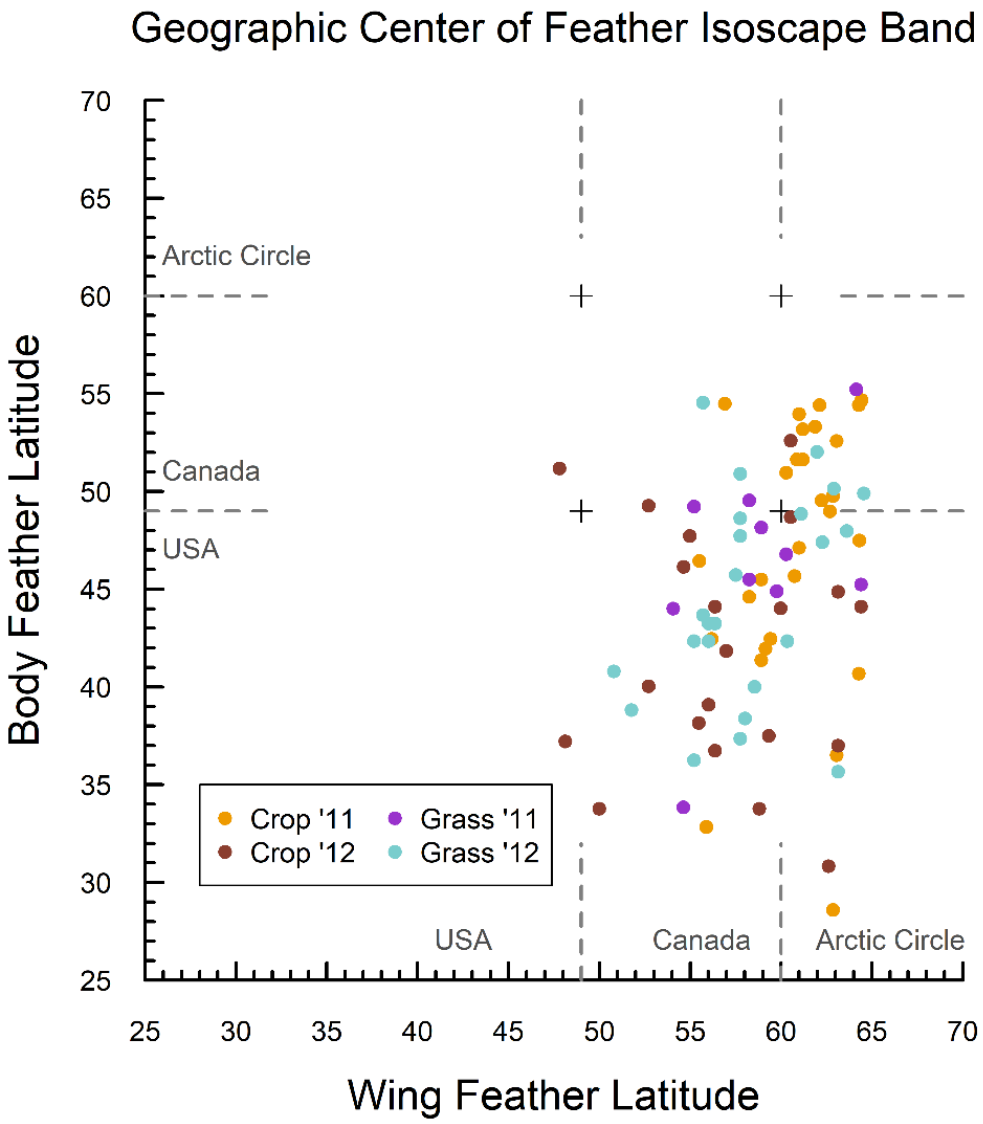

Figure B.4. Distribution of predicted latitudinal feather origins for wing and body feathers as derived using center of gravity of probabilistic isotopic assignment using a hydrogen isoscape. Nesting landscape type at capture is indicated by colors.

APPENDIX C: NORTHERN PINTAIL DUCKLING SURVIVAL ANALYSIS MODEL SELECTION TABLES

Table C.1. Full model selection tables for landscape survival analysis of northern pintail ducklings in Saskatchewan, 2011 – 2012. For details see Table 5.2.

Model Terms	k*	$QAIC_c$†	$\Delta QAIC_c$‡	w_i*	-2 Log Lik**
A) Study Site					
AGE + LAND + HATD	4	607.31	0.00	0.65	1791.92
AGE + GRSS + HATD	4	611.47	4.16	0.08	1804.37
AGE + HATD	3	612.11	4.80	0.06	1812.25
AGE + LAND	3	612.28	4.97	0.05	1812.77
AGE + WETL + HATD	4	612.87	5.56	0.04	1808.55
AGE + LAND + WETL	4	614.27	6.96	0.02	1812.73
AGE	2	614.51	7.20	0.02	1825.41
AGE + GRSS	3	614.70	7.39	0.02	1820.01
AGE + WETL	3	615.09	7.78	0.01	1821.17
AGE + GRSS + WETL	4	616.06	8.75	0.01	1818.09
AGE + YEAR	3	616.30	8.99	0.01	1824.78
NULL	1	736.70	129.39	0.00	2196.74
B) Nesting Habitat					
AGE + HAB + HATD	6	606.12	0.00	0.80	1776.40
AGE + HAB	5	609.84	3.72	0.12	1793.51
AGE + HATD	3	612.11	5.98	0.04	1812.24
AGE + WW + HATD	4	613.83	7.70	0.02	1811.41
AGE	2	614.51	8.38	0.01	1825.41
AGE + WW	3	615.55	9.42	0.01	1822.54
NULL	1	736.70	130.57	0.00	2196.74
C) Brood Route					
AGE + WT3 + PPC + EDW	5	585.79	0.00	0.66	1721.58
AGE + WT3 + EDW	4	589.55	3.77	0.10	1738.83
AGE + HATD + WT3 + EDW	5	590.30	4.51	0.07	1735.08
AGE + WT3 + EDG + EDW	5	590.67	4.88	0.06	1736.19
AGE + WT3 + EDW + YR	5	590.83	5.05	0.05	1736.67
AGE + PWW + WT3 + EDW	5	591.19	5.40	0.04	1737.73
AGE + PWW + PPC + EDW	5	594.49	8.71	0.01	1747.62

AGE + HATD + WT3 + PPC	5	596.87	11.09	0.00	1754.73
AGE + HATD + PPC + EDW	5	598.38	12.59	0.00	1759.22
AGE + HATD + WT3 + EDG	5	599.57	13.79	0.00	1762.80
AGE + PPC + EDW	4	600.07	14.28	0.00	1770.26
AGE + PWW + HATD + PPC	5	600.74	14.96	0.00	1766.30
AGE + PPC + EDG + EDW	5	601.81	16.03	0.00	1769.50
AGE + PPC + EDW + YR	5	601.84	16.06	0.00	1769.59
AGE + HATD + WT3	4	602.39	16.61	0.00	1777.22
AGE + PWW + WT3 + PPC	5	602.41	16.62	0.00	1771.28
AGE + WT3 + PPC	4	602.44	16.65	0.00	1777.36
AGE + WT3 + PPC + YR	5	603.51	17.73	0.00	1774.59
AGE + HATD + WT3 + YR	5	603.64	17.85	0.00	1774.97
AGE + HATD + PPC	4	604.06	18.27	0.00	1782.20
AGE + WT3 + PPC + EDG	5	604.24	18.45	0.00	1776.75
AGE + HATD + PPC + YR	5	604.28	18.50	0.00	1776.89
AGE + PWW + HATD + WT3	5	604.39	18.60	0.00	1777.20
AGE + HATD + EDW + YR	5	604.75	18.96	0.00	1778.28
AGE + WT3 + EDG	4	604.90	19.12	0.00	1784.73
AGE + WT3	3	605.03	19.24	0.00	1791.09
AGE + HATD + PPC + EDG	5	605.45	19.66	0.00	1780.38
AGE + HATD + EDG + EDW	5	605.84	20.06	0.00	1781.55
AGE + PWW + WT3 + EDG	5	605.96	20.18	0.00	1781.91
AGE + WT3 + EDG + YR	5	606.14	20.36	0.00	1782.45
AGE + PWW + EDG + EDW	5	606.29	20.50	0.00	1782.87
AGE + WT3 + YR	4	606.55	20.76	0.00	1789.64
AGE + EDW	3	606.76	20.97	0.00	1796.26
AGE + PWW + WT3	4	606.92	21.14	0.00	1790.77
AGE + HATD + EDW	4	606.98	21.19	0.00	1790.92
AGE + PWW + PPC	4	607.00	21.21	0.00	1791.00
AGE + EDG + EDW	4	607.04	21.25	0.00	1791.10
AGE + PWW + PPC + YR	5	607.89	22.10	0.00	1787.66
AGE + PWW + EDW	4	607.92	22.13	0.00	1793.73
AGE + EDW + YR	4	607.99	22.20	0.00	1793.95
AGE + PWW + HATD + EDG	5	608.10	22.31	0.00	1788.29
AGE + PWW + HATD + EDW	5	608.28	22.49	0.00	1788.83
AGE + PWW + WT3 + YR	5	608.44	22.66	0.00	1789.32

AGE + PWW + PPC + EDG	5	608.55	22.76	0.00	1789.64
AGE + EDG + EDW + YR	5	608.61	22.82	0.00	1789.81
AGE + HATD + EDG	4	608.85	23.07	0.00	1796.54
AGE + HATD + EDG + YR	5	608.94	23.15	0.00	1790.81
AGE + PWW + EDW + YR	5	609.14	23.35	0.00	1791.40
AGE + PPC	3	609.34	23.55	0.00	1803.98
AGE + PPC + YR	4	610.73	24.95	0.00	1802.16
AGE + PPC + EDG	4	611.24	25.45	0.00	1803.66
AGE + HATD	3	612.11	26.32	0.00	1812.25
AGE + PPC + EDG + YR	5	612.62	26.83	0.00	1801.80
AGE + HATD + YR	4	612.89	27.11	0.00	1808.61
AGE + PWW + EDG	4	613.54	27.75	0.00	1810.55
AGE + EDG	3	613.64	27.86	0.00	1816.84
AGE + PWW + HATD	4	613.83	28.04	0.00	1811.41
AGE	2	614.51	28.72	0.00	1825.41
AGE + PWW + HATD + YR	5	614.73	28.95	0.00	1808.13
AGE + PWW + EDG + YR	5	614.96	29.17	0.00	1808.81
AGE + EDG + YR	4	615.25	29.46	0.00	1815.66
AGE + PWW	3	616.12	30.33	0.00	1824.25
AGE + YR	3	616.30	30.51	0.00	1824.78
AGE + PWW + YR	4	617.88	32.10	0.00	1823.54

* Number of estimable parameters
† Akaike's Information Criterion adjusted for sample size and overdispersion
‡ Difference in QAICc compared to the best-approximating model
⁑ Model weight
** -2 x Log-Likelihood

APPENDIX D: MALLARD ASSESSMENT SITE DESCRIPTIONS

Table D.1. Location, area, habitat composition and moisture indices (Palmer Drought Severity Index, Pond Index) for study sites in the Canadian Prairie Parklands, 1993 – 2000.

Study area	Year	Location			Area (km^2)	Habitat area (%)						Moisture Index	
		Prov.	Lat.	Long.		Grass	Crop	Hay	Planted Cover	Wetland	Other	Pond Index	PDSI
Allan Hills E.	1999	SK	51.64	-105.94	65.8	16.9	37.1	5.4	18.8	13.5	7.4	1.29	0.70
Allan Hills N.	2000	SK	51.72	-106.22	66.4	6.6	58.8	4.2	7.4	10.4	9.8	-0.79	-0.93
Baldur	1996	MB	49.42	-99.33	67.3	16.9	29.1	5.8	6.6	20.2	20.7	1.42	-0.33
Donalda	1998	AB	52.54	-112.61	66.1	10.5	51.6	6.9	4.2	15.2	8.9	-0.62	-2.86
Elnora	1997	AB	52.04	-113.24	66.2	43.3	9.3	6.6	0.0	11.1	28.9	0.77	0.19
Erskine	1994	AB	52.32	-112.93	68.4	33.8	34.4	6.0	0.0	12.2	11.6	0.81	-1.10
Farrerdale	1998	SK	51.50	-105.86	65.9	21.8	62.1	1.7	0.0	6.8	5.6	-0.49	-3.93
Hamitoa	1993	MB	50.25	-100.69	80.5	3.1	77.5	0.3	0.0	5.6	9.9	-0.88	-2.11
Hay Lakes	1999	AB	53.19	-112.95	65.9	22.3	29.3	14.9	0.9	11.8	16.9	0.03	-2.13
Homefield	2000	MB	49.19	-99.51	68.0	19.3	24.5	9.2	7.6	31.9	5.1	-0.23	-0.66
Jumping Deer Ck.	1998	SK	51.23	-104.12	65.9	17.2	23.8	4.5	13.3	17.0	23.6	1.12	-3.02
Kutawa Lk.	1995	SK	51.42	-104.19	68.0	14.4	56.4	3.1	0.0	14.7	10.7	1.60	0.42
Leask	2000	SK	53.06	-106.83	65.2	12.7	53.4	4.9	0.4	15.8	11.7	-0.64	-1.43
Mixburn	1997	AB	53.14	-111.38	65.9	15.9	45.7	5.2	6.1	15.8	10.9	2.45	0.51
Parkside	1996	SK	53.18	-106.54	66.1	13.8	58.1	7.9	0.4	8.0	11.0	1.54	0.50
Pine Lk.	1996	AB	52.19	-113.42	65.4	36.0	20.2	9.1	0.0	12.2	21.5	1.34	-0.06
Punnichy	1993	SK	51.34	-104.31	56.6	9.0	64.3	1.0	4.5	6.8	11.7	-0.75	-2.23
Red Willow	1999	AB	52.44	-112.68	65.7	18.9	21.6	17.4	10.0	14.5	15.9	-1.06	-0.90
Willowbrook	1997	SK	51.22	-102.91	67.0	12.5	53.0	5.4	1.7	9.7	15.9	0.60	-1.17